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Optimal Control of Species Augmentation Conservation Strategies

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To the Graduate Council:

I am submitting herewith a dissertation written by Erin Nicole Bodine entitled "Optimal Control of Species Augmentation Conservation Strategies." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Mathematics.

Suzanne Lenhart, Major Professor

We have read this dissertation and recommend its acceptance:

Louis Gross, Charles Collins, Graham Hickling

Accepted for the Council:

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Optimal Control of Species Augmentation Conservation Strategies

A Dissertation

Presented for the

Doctor of Philosophy

Degree

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Erin Nicole Bodine

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Dedication

I dedicate this dissertation and the completion of my graduate education to my parents Mark and Christine Bodine, and to my husband Mac Bryan Barnes. Without their support, guidance, and encouragement over the years, reaching these goals would not have been possible. I thank each of them for always believing in me and in my academic abilities.

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Abstract

Species augmentation is a method of reducing species loss via augmenting declining or threatened populations with individuals from captive-bred or stable, wild populations. In this dissertation, species augmentation is analyzed in an optimal control setting to determine the optimal augmentation strategies given various constraints and settings. In each setting, we consider the effects on both the target/endangered population and a reserve population from which the individuals translocated in the augmentation are harvested. Four different optimal control formulations are explored. The first two optimal control formulations model the underlying population dynamics with a system of ordinary differential equations. Each of these two formulations utilizes a different function to model the cost of augmentation. For each optimal control formulation we find a characterization for the optimal control and show numerical results for scenarios of different illustrative parameter sets.

The second two optimal control formulations model the underlying population dynamics with systems of discrete difference equations. The difference between these two optimal control formulations is the order in which events occur within each time step in the population models. In the first formulation the population is augmented before the natural growing season in each time step (augment then grow model), whereas in the second formulation the population is augmented after the natural growing season in each time step (grow then augment model). These two discrete time models, which differ only in their order of events, lead to structurally different models. The formulation with the augment then grow model cannot utilize discrete time optimal control theory and a brute force method of finding the optimal augmentation strategy is used. The formulation with the grow then augment model does utilize optimal control theory and we find the characterization of the optimal control. For both formulations, we explore several scenarios of different illustrative parameter sets.

In each of the four optimal control formulations, the numerical results provide considerably more detail about the exact dynamics of optimal augmentation than can be readily intuited. The work presented here are the first steps toward building a general theory of population augmentation, which accounts for the complexities inherent in many conservation biology applications.

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Chapter 1

Introduction

Over the past three decades, much of ecological research has focused on biodiversity. Despite the efforts of many to protect and sustain certain species and ecosystems, there are thousands of species considered threatened or endangered [1]. One method of reducing species loss is to augment declining or threatened populations with individuals from captive-bred or stable, wild populations. This method is known as "species augmentation." Though the number of researchers calling for augmentation of threatened or endangered species has been increasing, and a handful of augmentation projects have been or are currently being carried out, there have been virtually no systematically developed theoretical or practical tools for studying and predicting the impact of species augmentation. Some key questions regarding augmentation are:

1. When is the optimal time to introduce individuals into a target endangered population?

2. How many individuals need to be added to the target population to meet certain objectives (e.g. sustainability over some period of time, some measure of increased genetic diversity, etc.)?

3. Will the target population require future augmentations in order to maintain those objectives?

4. At what location(s) should individuals be released when augmenting the target population such that the target population receives maximal benefit?

5. How do the dynamics of augmentation strategies change when considering the trade-off between tranlocating individuals into a wild, endangered population versus leaving the individuals there given that translocations/augmentations are not always successful and an endangered wild population may recover on its own?

Each of these questions requires developing an appropriate theoretical framework to analyze in general, so that each situation need not be considered separately. Mathematical results and corresponding tools have not been developed yet for modeling the dynamics of augmented populations and communities.

The goal of my research is to begin developing a framework to address the biological questions surrounding species augmentation, with the broader aim of providing mathematical modelers, ecologists, and natural resource managers with theory and tools for analyzing control strategies in augmented systems. By control here, I mean methods to effectively manage populations through appropriate augmentation. As a general augmentation theory is developed, the results can be readily adapted to a variety of specific cases.

1.1 Background

Recently, researchers working to conserve various species have begun to recommend species augmentation as a means to bring declining wild populations up to sustainable levels and to introduce greater genetic diversity to threatened and endangered populations. For example, a 2004 study of relative density and population size of a threatened grizzly bear population in Washington and British Columbia recommended augmentation after finding that natural recovery was highly unlikely [35]. A 1998 study of huemul deer species in South America recommended augmentation along with other conservation efforts to increase the range and total number of huemul which had been reduced to a single population in Central Chile [34]. A 2006 population viability analysis (PVA) of ocelots (*Leopardus pardalis*) found that a combination of different recovery strategies, including augmentation, are needed to reduce ocelot extinction probability [17]. Other studies recommending augmentation as a means to promote species recovery and prevent extinction include [19, 20, 24, 29, 31, 40].

In addition to such recommendations for augmentation, a handful of species augmentation projects have been executed and their level of success documented. Between July 1990 and October 1993, four female grizzly bears of cub bearing age were captured in British Columbia and translocated to the Cabinet Mountains in Montana for an augmentation effort [38]. As of 2004, three of the four females were still within their target release area, but none of the three had produced any cubs. In 2007, it was reported that there was genetic evidence that at least one of the original transplanted bears had reproduced [23]. In 2009, it was confirmed that one translocated female and her offspring were still in the target release area [43]. In 1995, eight female panthers (*Puma concolor*) were brought from Texas to augment the endangered Florida panther population in an effort to increase the low genetic diversity of the Florida panther population [27]. Since the augmentation effort, the panther population has increased from roughly 30 individuals to almost 100 and there is no evidence that individuals with Texas panther ancestry have inbreeding related defects [14, 27, 32].

Despite the growing need and use of species augmentation as a conservation tool, very little mathematical results or practical tools have been developed to study and predict the impact of species augmentation. The models developed to describe and predict the outcome of species augmentation, though potentially applicable to a wider range of species, do not attempt to develop any general mathematical theory for augmentation and instead focus solely on one species. Pfab and Witkowski constructed a population viability analysis which compared four management strategies, one of which was augmentation for the critically endangered succulent plant species *Euphorbia clivicola* confined to only two known populations in the Northern Province of South Africa [31]. Hearne and Swart constructed a non-linear differential equation model of the black rhinoceros (*Diceros bicornis*) in South Africa for which their simulations gave an indication of the number and age of animals which should be translocated to maximize the growth rate of the total rhino population in southern Africa [19]. Prior to the 1995 Florida panther augmentation, Hedrick developed a population genetics model to evaluate the potential for genetic restoration via augmentation and its specific applicability to the Florida panther case [20]. This model was then used as one of the justifications to proceed with the Florida panther augmentation project. Rout *et al.* developed a stochastic population model of the bridled nailtail wallaby (*Onychogalea fraenata*) and used decision theory and stochastic dynamic programming to determine an optimal translocation strategy of how many wallabies to augment each population, given the state of each population, in order to maximize the benefit to the entire species [36].

Optimal control theory has been applied to systems of ordinary differential equations and discrete time difference equations, modeling a variety of population scenarios. See for example, [15] for a predator-prey system, [37] for a harvesting problem for bears in a park-forest scenario, and [42] for control of pests. See the books by Eisen [10], Lenhart and Workman [44], and Sethi and Thompson [39] for other examples. My research presents the first applications of optimal control to model augmentation. We call attention to the recent paper on optimization for a linear augmentation model with discrete time and stage structure (Hodgson *et al.* [22]). We also call attention to Hearne and Swart's model for the optimal translocation of an age-structured black rhino population [19] where the strategies of maximizing the translocation rate and maximizing the growth of a newly established population are compared.

Many specific mathematical models and some general mathematical theory has been developed for augmenting natural predators of agricultural pests in an effort to control those pests. This form of species augmentation is generally referred to as *biological control*. Though some of the theory developed for biological control will be instructive in my research [18], biological control focuses on insect (or virus) species which generally require particular assumptions in the analysis that are quite different from problems of augmentation of threatened populations. Additionally, the control strategy used in biological control is to minimize a certain pest population, while the control strategy used in conservation resource management is to maximize some measure of a threatened or endangered species population. These differences in model structure and control strategy warrant the development of mathematical control theory specifically designed for species augmentation as well as development of practical methods to apply it as a conservation tool.

Note as well that the mathematical models and control theory needed for species augmentation as a conservation tool differ from standard metapopulation models. Standard metapopulation models allow for flow between two subpopulations of the same species. This usually assumes a constant flow or a periodic flow. However, species augmentation is implemented by translocating a certain number of individuals at a few discrete times, which is different mathematically than assuming a constant or periodic flow from one subpopulation to another. Though models developed for species augmentation as a conservation tool will still fall under the category of metapopulation models because they incorporate movement between subpopulations, the mathematics is inherently different from the standard metapopulation models due to the need to view this in an optimization and control framework.

The scientific interest and ecological importance of species augmentation as a conservation tool merits the development of a general mathematical control framework of species augmentation which will provide mathematical modelers, ecologists, and natural resource managers with theory and tools for analyzing control strategies in augmented systems.

1.2 The Allee Effect

In the 1930's Warder C. Allee wrote about the possibility of populations at low numbers having a positive relationship between any component of fitness and either the numbers or density of conspecifics [2, 3, 6, 8, 41]. Since then, this biological phenomenon has been referred to as the *Allee effect*. The general idea is that individuals in small populations will have lower reproduction and survival rates, but that these rates will increase with population size or density. The Allee effect is generally thought to disappear once population size or density is large enough and increased intraspecific competition (competition for resources among individuals within the population) occurs. The most obvious cause of the Allee effect in sexually reproducing species is the difficulty in finding mates at low population sizes [6]. Other causes could be the necessity of a minimal group size for finding food, preventing predator attacks, and rearing offspring [6, 8, 41].

A distinction is made between what is known as a *strong Allee effect* and a *weak Allee effect*. Populations exhibiting a strong Allee effect have a critical population size or density, below which the growth rate of the population is negative and above which the population growth rate is positive. Populations exhibiting a weak Allee effect have do not have this critical threshold [4].

Populations requiring augmentation are often populations small in size and on the decline. For endangered populations exhibiting a strong Allee effect, it is reasonable to assume the populations are currently below some critical density and currently have a negative growth rate. If these populations could be augmented to be above the critical density, they would begin to grow on their own.

The underlying population models presented in this dissertation are assumed to have both logistic growth and a strong Allee effect. We model a single population in continuous

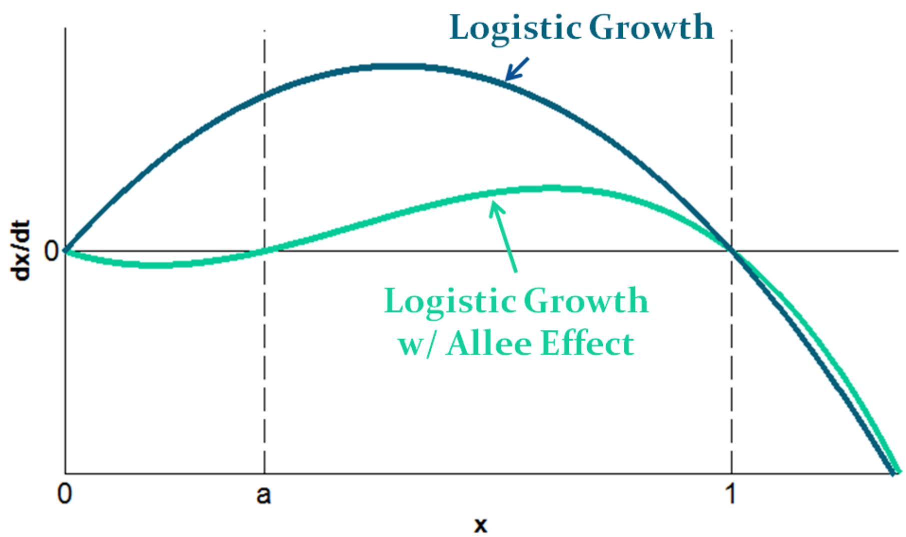


Figure 1.1: A plot of the population growth rate $\frac{dx}{dt}$ versus the population density x for both logistic growth $dx/dt = rx(1-x)$ and logistic growth with a strong Allee effect $dx/dt = rx(1-x)(x-a)$. With the Allee effect, the constant a is the critical threshold for growth for the population such for $0 < x < a$ the population has a negative growth rate, and for $a < x < 1$ the population has a positive growth rate.

time using the density equation

$$\frac{dx}{dt} = rx(1-x)(x-a) \tag{1.1}$$

where the population has been normalized with respect to its carrying capacity [25]. In Equation (1.1), r is the intrinsic growth rate of the population, and a is the critical threshold below which the population will have a negative growth rate. Notice that if the last term of the product on the right hand side of Equation (1.1) is removed, then only the standard (normalized) logistic growth equation, $dx/dt = rx(1-x)$, remains. It is known that for the normalized logistic growth equation, the equlibria are $x = 0$ (unstable), and $x = 1$ (stable). When we multiply by the term $(a-x)$, we add another equilibrium, $x = a$. Thus, for the population with both logistic growth and a strong Allee effect, the equlibria are $x = 0$ (stable), $x = a$ (unstable), and $x = 1$ (stable). Notice, the critical threshold for growth $x = a$ is an unstable equilibrium, but extinction $x = 0$ is now a stable equilibrium. Additionally, because the logistic growth is still included, $x = 1$ still represents the saturation level of the carrying capacity. For population densities greater than 1, the population will decline back down to its carrying capacity $x = 1$. Figure 1.1 shows a plot of the population growth rate, $\frac{dx}{dt}$, against the population density x both normalized logistic growth, and for normalized logistic growth with a strong Alee effect.

For the remainder of this dissertation, when we state that we are including the Allee effect, it is implied that we are using a strong Allee effect.

1.3 Optimal Control Theory

In an optimal control problem, the values of controls are adjusted to achieve a goal within a dynamic system. The underlying dynamic system can take a variety of forms: ordinary differential equations, partial differential equations, discrete difference equations, stochastic differential equations, or integrodifference equations. Here, we focus on optimal control formulations whose underlying dynamics are defined by either ordinary differential equations or discrete difference equations.

1.3.1 Ordinary Differential Equation State Systems

In the control of a single ordinary differential equation (ODE), let $u(t)$ be the control and $x(t)$ be the state which is defined by an ODE

$$\frac{dx}{dt} = g(t, x(t), u(t)).$$

Notice the rate of change of the state depends on the function $u(t)$. It is assumed that both $u(t)$ and $x(t)$ affect the goal, which we call the objective functional. Consider the optimal control problem where the objective functional is

$$\max_u \left[\phi(x(T)) + \int_0^T f(t, x(t), u(t))\ dt \right] \tag{1.2}$$

subject to

$$\frac{dx}{dt} = g(t, x(t), u(t)) \tag{1.3}$$

where

$$x(0) = x_0 \tag{1.4}$$

and $x(T)$ is free. The term, $\phi(x(T))$, represents a type of *salvage* term. We may, for example, want the state x to be large at the final time T. We assume that the controls are piecewise continuous functions with values in a set U_1. However, one can also use Lebesgue measurable functions. The control that maximizes the objective functional is denoted $u^*(t)$, and is called the optimal control. When $u^*(t)$ is substituted into the state ODE in Equation (1.3), we obtain the corresponding optimal state, $x^*(t)$. We call $(u^*(t), x^*(t))$ the optimal pair.

Around 1950, Lev Pontryagin and his collaborators developed necessary conditions for optimal control theory. That is, if $(u^*(t), x^*(t))$ is an optimal pair, then these conditions hold. The key idea was introducing the adjoint function to attached the ODE to the objective functional. This idea is similar to Lagrange multipliers which attach the constraints when finding the maximum of a function in multi-dimensional calculus subject to some equation constraints. The first order necessary conditions in the simplest form are given by Pontryagin's Maximum Principle [33]. Before applying this principle, one should show that an optimal control exists using a compactness argument which depends on the specific set of controls used (usually piecewise continuous or Lebesgue measurable functions). After showing the objective functional is bounded for all controls, once can construct a maximizing sequence of controls and corresponding states sequences to show convergence in the appropriate space. See [11, 13] and Chapter 2 for details and examples of existence results.

Assume, f, g, and ϕ are differentiable functions of their arguments and f and g are concave in u.

Theorem 1.3.1 (Pontryagin's Maximum Principle). *If $u^*(t)$ and $x^*(t)$ are optimal for the problem defined in Equations (1.2)-(1.4), then there exists an adjoint variable $\lambda(t)$ such that*

$$H(t, x^*(t), u(t), \lambda(t)) \leq H(t, x^*(t), u^*(t), \lambda(t)),$$

at each time, for all u with values in U_1 where the Hamiltonian H is defined by

$$H(t, x(t), u(t), \lambda(t)) = f(t, x(t), u(t)) + \lambda(t)g(t, x(t), u(t)),$$

and the adjoint function is defined by the ODE

$$\frac{d\lambda}{dt} = -\frac{\partial H}{\partial x}, \quad \lambda(T) = \frac{d\phi}{dx}(x(T)).$$

Note that the final time condition on the adjoint variable is called the *transversality condition*. Pontryagin's Maximum Principle converts the problem of finding the control that maximizes the objective functional subject to the state ODE and initial condition to the problem of optimizing the Hamiltonian pointwise. Note that this theorem is stated for the simplest case where there are no constraints (like upper and lower bounds) on the controls.

This version of Pontryagin's Maximum Principle is for an optimal control formulation with one control and one state variable. This principle has an extension to multiple states and controls. For each state variable, we introduce one corresponding adjoint variable. If we have n state variables,

$$\begin{aligned} x_1(t) &= g_1(t, x_1(t), \ldots, x_n(t), u(t)) \\ &\vdots \\ x_n(t) &= g_1(t, x_1(t), \ldots, x_n(t), u(t)) \end{aligned}$$

then we introduce adjoints, $\lambda_1(t), \ldots, \lambda_n(t)$. Suppose the objective function becomes

$$\max_u \left[\phi\left(x(T), \ldots, x_n(T)\right) + \int_0^T f(t, x_1(t), \ldots, x_n(t), u(t))\, dt \right].$$

Then the Hamiltonian becomes

$$\begin{aligned}H(t, x_1(t), \ldots, x_n(t), u(t), \lambda(t)) &= f(t, x_1(t), \ldots, x_n(t), u(t)) \\ &\quad +\lambda_1(t) g_1(t, x_1(t), \ldots, x_n(t), u(t)) \\ &\quad + \cdots + \lambda_n(t) g_n(t, x_1(t), \ldots, x_n(t), u(t)),\end{aligned}$$

and the adjoint variables are defined by the ODEs and transversality conditions

$$\begin{aligned}\frac{d\lambda_1}{dt} &= -\frac{\partial H}{\partial x_1},\ \lambda_1(T) = \frac{d\phi}{dx_1}\left(x_1(T), \ldots, x_n(T)\right) \\ &\vdots \\ \frac{d\lambda_n}{dt} &= -\frac{\partial H}{\partial x_n},\ \lambda_n(T) = \frac{d\phi}{dx_n}\left(x_1(T), \ldots, x_n(T)\right).\end{aligned}$$

1.3.2 Discrete Time Difference Equation State Systems

In the control of a single discrete difference equation, let $u = (u_0, u_1, \ldots, u_{T-1})$ be the control and $x = (x_0, x_1, \ldots, x_T)$ be the state which is defined by a difference equation

$$x_{k+1} = g(k, x_k, u_k) \text{ with initial state } x_0,$$

for $k = 0, 1, 2, \ldots, T-1$. Notice the state at a given time $k+1$ step depends on the control at time step k. Additionally, notice than the state has one more component that the control. It is assumed that both $u(t)$ and $x(t)$ affect the goal, which we call the objective functional. Consider the optimal control problem where the objective functional is

$$\max_u \left[\phi(x_T) + \sum_{k=0}^{T-1} f(k, x_k, u_k)\right] \tag{1.5}$$

subject to

$$x_{k+1} = g(k, x_k, u_k) \tag{1.6}$$

where x_0 is the initial state and x_T is free. The term $\phi(x_T)$ represents a type of salvage term. The control that maximizes the objective functional is denoted u^*, and is called the optimal control. When u^* is substituted into the state difference equation in Equation 1.6, we obtain the corresponding optimal state, x^*.

Using a generalization of Pontryagin's Maximum Principle [33] we can derive necessary conditions that an optimal control and corresponding state must satisfy, similar to when the underlying states are described using ODEs (see Section 1.3.1). We assume f, g, and ϕ are differentiable functions of their arguments and f and g are concave in u.

Theorem 1.3.2 (Pontryagin's Maximum Principle for Discrete Time). *If u^* and x^* are optimal for the problem defined in Equations (1.5)-(1.6), then there exists an adjoint* *variable* $\lambda = (\lambda_0, \lambda_1, \dots, \lambda_T)$ *such that*

$$H_k(k, x_k^*, u_k, \lambda_k) \leq H_k(k, x_k^*, u_k^*, \lambda_k),$$

at each time step k*, for all* u *where the Hamiltonian at time step* k *is defined by*

$$H_k = f(k, x_k, u_k) + \lambda_{k+1} g(k, x_k, u_k),$$

and the adjoint function is defined by the difference equation

$$\lambda_k = -\frac{\partial H_k}{\partial x_k}, \quad \lambda_T = \frac{d\phi}{dx}(x_T).$$

Note, as in the continuous time case, the final time condition on the adjoint variable is called the *transversality condition*. Again, as in the continuous time case, we see that Pontryagin's Maximum Principle converts the problem of finding the control that maximizes the objective functional subject to the state difference equation with initial state to the problem of optimizing the Hamiltonian at each step with respect to the control value at that step. Notice the indexing of the adjoint in the Hamiltonian; it is one step ahead of the other terms.

Note, in Chapter 4 we will see an example of an optimal control formulation where the concavity condition of f is not met and we cannot use Pontryagin's Maximum Principle to obtain the necessary conditions.

The version of Pontryagin's Maximum Principle given in Theorem 1.3.2 is for an optimal control formulation with one control and one state. As with the continuous time case, for every state variable, we introduce one corresponding adjoint variable. If we have n state variables,

$$\begin{aligned} x_{k+1}^1 &= g^1(k, x_k^1, \dots, x_k^n, u_k) \\ &\vdots \\ x_{k+1}^n &= g^n(k, x_k^1, \dots, x_k^n, u_k), \end{aligned}$$

then we introduce adjoints $\lambda^1, \dots, \lambda^n$. Suppose the objective functional becomes

$$\max_u \left[\phi\left(x_T^1, \dots, x_T^n\right) + \sum_{k=0}^{T-1} f(k, x_k^1, \dots, x_k^n, u_k) \right].$$

Then the Hamiltonian becomes

$$H_k = f(k, x_k^1, \dots, x_k^n, u_k) + \lambda_k^1 g^1(k, x_k^1, \dots, x_k^n, u_k) + \dots + \lambda_k^n g^n(k, x_k^1, \dots, x_k^n, u_k)$$

and the adjoint variables are defined by the difference equations and transversality conditions

$$\begin{aligned}
\lambda_k^1 &= \frac{\partial H_k}{\partial x_k^1},\ \lambda_T^1 = \frac{d\phi}{dx^1}\left(x_T^1, \ldots, x_T^n\right) \\
&\vdots \\
\lambda_k^n &= \frac{\partial H_k}{\partial x_k^n},\ \lambda_T^n = \frac{d\phi}{dx^n}\left(x_T^1, \ldots, x_T^n\right).
\end{aligned}$$

1.4 Numerical Methods

Within Chapters 2 - 5, given each optimal control formulation we numerically find the control that maximizes the objective functional. In Chapters 2, 3, and 5 we use a numerical method called the forward-backwards sweep for finding the optimal control. In Chapter 4 we use a simple brute force method to directly find the optimal control vector that maximizes the objective functional.

1.4.1 Forward-Backwards Sweep Method

This method can be used for optimal control formulations whose underlying states dynamics are in continuous or discrete time. If a continuous time model is used, then discrete numerical approximations are made for the state variables, adjoint variable, and the control function. Thus, whether the underlying state equations are continuous or discrete, the forward-backwards sweep method denotes the states, adjoints, and controls as vectors where each component of the vector is the state, adjoint, or control function at a particular time step (within the time horizon). The forward-backwards sweep method starts by making an initial guess for the control vector, and then solves the state equations forward in time since the state equations have initial conditions. Next, using the guessed control vector and the newly found state vectors, the adjoint equations are solved backwards in time since the adjoint equations have terminal conditions (the transversality conditions). If the state and adjoint equations are continuous in time, then these equation are solved using the Runge-Kutta 4 method (a standard method for solving systems of ordinary differential equations). If the state and adjoint equations are discrete in time, then the these equations are solved iteratively through time using the discrete difference equations. Again, note the adjoint equations will be solved iteratively backwards through time. At this point, the control vector is updated using the characterization of the optimal control and the values for the state and adjoint variables. This updated control is now the new guess for the control vector. The process is now repeated until the successive iterates of control vectors are sufficiently close. If u is the current control vector and u_{old} is the control vector from the previous iteration, then we say the control vectors are sufficiently close when

$$\frac{||u - u_{old}||_1}{||u||_1} < \delta$$

at each point where δ is a set convergence threshold and

$$||u||_1 = \sum_{i=0}^{T-1} |u_i| \, .$$

The convergence of such an iterative method is based on the work of Hackbush [16]. Examples using this method can be found in [12, 21, 37].

1.4.2 Direct Maximization of the Objective Functional

In Chapter 4 we find that we must resort to a numerical method that directly maximizes the objective functional. To do this, we discretize the range of the control and search for the control vector that maximizes the objective functional. We first define how the control space will be discretized. Given that discretization, we next evaluate the objective functional for all possible permutations of the components of the control vector. Since the objective functional depends not only on the control but on the state variables at the final time, the state equations are solved iteratively, given the control, to find the values of the state equations at the final time. In evaluating the objective functional for each control, we can determine which control vector maximizes the objective functional. The control vector that maximizes the objective function is the optimal control.

1.5 Overview of the Optimal Control Problems

Each of the optimal control problems we consider in the following chapters start with the same premise. We assume there is an endangered population (which we refer to as the target population) that is presently declining. There also exists a reserve population from which individuals can be harvested and translocated into the target population (this is the process of augmentation). We assume that we can control the rate or proportion (of the reserve) at which individuals are translocated from the reserve population to the target population over a set time horizon. Additionally, we assume there is some cost associated with augmentation (time, money, resources, effort, etc.). There are two ways in which we characterize the costs associated with augmentation. First, we assume that there could be costs which increase linearly as the rate/proportion of the reserve population translocated increases. Secondly, we recognize that there could be costs which increase in a nonlinear fashion as the rate/proportion of the reserve population translocated increases. We capture these nonlinear increases in costs by assuming costs which increase quadratically as the rate/proportion of the reserve population translocated increases. The objective for each optimal control problem is to find the the control that maximizes the target population at the final time (end of time horizon), maximizes the reserve population at the final time (though weighted as less important than maximizing the target population), and minimizes the costs associated with augmentation. In Chapters 2 - 5 we explore the impact on the optimal control of using continuous versus discrete time to model the underlying dynamics of the target and reserve populations, the difference the order of events makes within a discrete time model, and the role that linear versus quadratic increases in costs makes. In Chapter 2, we investigate the optimal control formulation which assumes the target and reserve populations can be modeled with ODEs and the costs associated with augmentation increase quadratically as the rate/proportion of the reserve population translocated increases. In Chapter 3, we investigate an optimal control formulation which is similar to that explored in Chapter 2, but assumes the costs associated with augmentation increase linearly as the rate/proportion of the reserve population translocated increases. In Chapters 4 and 5, we turn to optimal control formulations which assume the target and reserve populations can be modeled with discrete time difference equations. The main difference between the two chapters is the order in which the events of each time step occur. Chapter 4 investigates the optimal control formulation in which the discrete time model assumes the order of events within each time step is that augmentation occurs before natural population growth. Additionally, Chapter 4 assumes that the costs associated with augmentation increase linearly and/or quadratically as the rate/proportion of the reserve population translocated increases. In Chapter 5, we investigate the optimal control formulation in which the order of events within each time step is that the natural population growth occurs before the augmentation. Additionally, Chapter 5 assumes that the costs associated with augmentation increase linearly and quadratically or only quadratically as the rate/proportion of the reserve population translocated increases.

Lastly, the final chapter, Chapter 6 describes what future extensions of these optimal control formulations are still left to be explored.

Chapter 2

Continuous Time Model with Quadratic Objective Functional

Consider two populations of the same species: N, a target/endangered population, and R, a reserve population. We assume that, at the initial time, the endangered population is declining due to small population size, i.e. there is some critical population size, below which the population declines to extinction. For the reserve population to be a viable source for harvesting individuals with which to augment the target population, it must be growing at the initial time, but it is also assumed to have a lower threshold for population growth which could be crossed due to over harvesting. Therefore, each of these populations are assumed to grow according to a normalized Allee effect model [25], in which aKN and bKR are the critical population sizes for growth for the target and reserve populations, respectively. The control u is the rate at which individuals are moved from the reserve population to the target population. Thus, the populations are modeled by the equations

$$\begin{aligned}
\frac{dN}{dt} &= rN\left(1-\frac{N}{K_N}\right)\left(\frac{N}{K_N}-a\right)+uR \\
\frac{dR}{dt} &= sR\left(1-\frac{R}{K_R}\right)\left(\frac{R}{K_R}-b\right)-uR
\end{aligned}$$

where r and s are the intrinsic growth rates of N and R, respectively, K_N and K_R are the carrying capacities of N and R, respectively, and aK_N and bK_R are the thresholds for population growth for N and R, respectively. Here we assume there is no net loss of population due to augmentation efforts. Additionally, we assume that the intrinsic growth rates r and s can be different in value. The difference could be due to different environmental conditions where the target and reserve populations are located, or could be due to difference in the underlying genetics of the two populations. The latter would be especially true if the target and reserve populations were different subspecies of the same species.

Rescaling the two populations with respect to their carrying capacities $\left(x \equiv \frac{N}{K_N}\right.$ and $\left.y \equiv \frac{R}{K_R}\right)$ gives

$$\begin{aligned}\frac{dx}{dt} &= rx(1-x)(x-a)+puy\\ \frac{dy}{dt} &= sy(1-y)(y-b)-uy\end{aligned}$$

where $p = K_R/K_N$, i.e. the ratio of the reserve carrying capacity to the target carrying capacity.

We assume the objective of augmentation is to maximize the target population at a given final time while minimizing the cost. This assumes there is cost associated with translocating an individual from the reserve population, and that it would be ideal to minimize this cost. We assume this cost to be a quadratic function of the fraction translocated. We assume that the total population $(x+y)$ is to be maximized at the final time, with different relative weights applied to the reserve and target populations. We assume it is not as important to maximize the reserve population as it is the target population by the final time. Additionally, we assume that the target population x has an initial density x_0 below its minimum threshold for growth $0 < a < 1$, and that the reserve population y has an initial density y_0 above its minimum threshold for growth $0 < b < 1$. Thus, $x_0 < a$ and $y_0 > b$.

Thus, the optimal control formulation is

$$\max_{u \in U}\left[x(t_1) + By(t_1) - \int_{t_0}^{t_1}\big(A_1u^2(t) + A_2u(t)\big)\,dt\right] \tag{2.1}$$

where

$$U = \{u : [t_0, t_1] \to [0,1] \mid u \text{ Lebesgue measurable}\} \tag{2.2}$$

and

$$\begin{aligned}x'(t) &= rx(1-x)(x-a)+puy, \quad x(t_0) = x_0 \text{ where } 0 < x_0 < a < 1 && (2.3)\\ y'(t) &= sy(1-y)(y-b)-uy, \quad y(t_0) = y_0 \text{ where } 0 < b < y_0 < 1 && (2.4)\end{aligned}$$

and a, b, t_0, t_1, x_0, y_0, r, s, A_2, and B are all non-negative constants, $A_1 > 0$ and $0 \le B \le 1$. The objective functional seeks to maximize the two populations at the final time while minimizing the cost associated with translocating an individual from the reserve population to the target population. Here the cost is a weighted sum of terms linear and quadratic in the control. The weight factor B balances out the relative importance of maximizing the reserve population. We assume the cost term is a nonlinear function of the control and use a quadratic cost to account for nonlinear increases in costs of translocation as the fraction translocated per unit time increase. We assume x_0 and y_0 are positive. Within this formulation, we seek to find the control u^* that maximizes the objective functional

$$J(u) = x(t_1) + By(t_1) - \int_{t_0}^{t_1} \left(A_1 u^2(t) + A_2 u(t)\right) dt. \tag{2.5}$$

In several places in the subsequent analysis we will use the fact that

$$\begin{aligned} x(1-x)(x-a) &= -x^3 + (1+a)x^2 - ax, \quad \text{and} && (2.6)\\ y(1-y)(y-b) &= -y^3 + (1+b)y^2 - by. && (2.7) \end{aligned}$$

2.1 Boundedness of the State Variables

Here we show that the state variables are uniformly bounded. The following theorem will be used later in the proofs of both the existence and uniqueness of the optimal control for the optimal control formulation, Equations (2.1)-(2.4).

Theorem 2.1.1. *Given the state equations for x and y defined in Equations (2.3) and (2.4) there exist constants $C_1, C_2 > 0$ such that $0 \leq y(t) \leq C_1$ and $0 \leq x(t) \leq C_2$ for all $t \in [t_0, t_1]$.*

Proof: Given the state equation for y defined in Equations (2.4) with initial conditions $0 < b < y_0 < 1$, observe that $y = 0$ is an equilibria for Equation (2.4). Therefore, since y' is continuous and $y_0 > 0$, then $y(t) > 0$ for all $t \in [t_0, t_1]$. Now, notice that the function

$$f(y) = (1-y)(y-b) = -y^2 + (1+b)y - b$$

attains its maximum value at $y = \frac{b+1}{2}$. Since $0 < b < 1$,

$$0 < \frac{b+1}{2} < 1.$$

Furthermore,

$$f\left(\frac{b+1}{2}\right) = \frac{(b-1)^2}{4}.$$

Again, since $0 < b < 1$,

$$0 < \frac{(b-1)^2}{4} < 1.$$

Given Equation 2.4, we have the following inequality

$$\begin{aligned} y' &= sy(1-y)(y-b) - uy \\ &\leq sy(1-y)(y-b) \\ &\leq sy\left[\frac{(b-1)^2}{4}\right]. \end{aligned}$$

Let $K_1 = \frac{s}{4}(b-1)^2$. Then $K_1 \geq 0$ and we have the inequality,

$$y' \leq K_1 y.$$

One can show the solution to this differential inequality satisfies

$$y(t) \leq y_0 e^{K_1(t-t_0)} \leq y_0 e^{K_1(t_1-t_0)},$$

when $y_0 > 0$. Since $0 < y(t) \leq y_0 e^{K_1(t_1-t_0)}$ for $t \in [t_0, t_1]$ when $y_0 > 0$, then $y(t)$ is bounded for any $t \in [t_0, t_1]$ with $y_0 > 0$. Specifically, for each $t \in [t_0, t_1]$, $0 \leq y(t) \leq C_1$ where $C_1 = y_0 e^{K_1(t_1-t_0)}$.

Next, notice that the function

$$g(x) = (x-1)(x-a)$$

attains its minimum value at $x = \frac{1+a}{2}$ and that

$$g\left(\frac{1+a}{2}\right) = -\frac{(1-a)^2}{4}.$$

Now, given the state equation for x defined by Equation (2.3) with initial condition $0 < x_0 < a < 1$, and given that $y(t) > 0$ as shown above, then

$$\begin{aligned} x' &= rx(1-x)(x-a) + puy \\ &= -rx(x-1)(x-a) + puy \\ &\geq -rx\left[(x-1)(x-a)\right] \\ &\geq -rx\left[-\frac{(1-a)^2}{4}\right] \\ &= \frac{r(1-a)^2}{4}x. \end{aligned}$$

Let, $K_2 = \frac{r(1-a)^2}{4}$. Then, $K_2 > 0$ and we have the inequality,

$$x' \geq K_2 x.$$

One can show that the solution to this differential inequality satisfies

$$x(t) \geq x_0 e^{K_2(t-t_0)} > 0,$$

for $t \in [t_0, t_1]$. Thus, $x(t) > 0$ for all $t \in [t_0, t_1]$.

Next, notice the function

$$h(x) = (1-x)(x-a) = -x^2 + (1+a)x - a$$

attains its maximum value at $x = \frac{a+1}{2}$. Since $0 < a < 1$,

$$0 < \frac{a+1}{2} < 1.$$

Furthermore,

$$h\left(\frac{a+1}{2}\right) = \frac{(a-1)^2}{4}.$$

Again, since $0 < a < 1$,

$$0 < \frac{(a-1)^2}{4} < 1.$$

Given Equation 2.3, we have the following inequality

$$\begin{aligned} x' &= rx(1-x)(x-a) + puy \\ &\leq rx\left[\frac{(a-1)^2}{4}\right] + pC_1 \end{aligned}$$

Let $K_3 = pC_1 > 0$, then we have the inequality

$$x' \leq K_2 x + K_3.$$

One can show the solution to this differential inequality satisfies

$$x(t) \leq x_0 e^{K_2(t-t_0)} - \frac{K_3}{K_2}\left(1 - e^{K_2(t-t_0)}\right) \leq \left(x_0 + \frac{K_3}{K_2}\right) e^{K_2(t_1-t_0)},$$

when $x_0 > 0$. Since $0 < x(t) \leq \left(x_0 + \frac{K_3}{K_2}\right) e^{K_2(t_1-t_0)}$ for $t \in [t_0, t_1]$ when $x_0 > 0$, then $x(t)$ is bounded for any finite $t \in [t_0, t_1]$. Specifically, for each $t \in [t_0, t_1]$, $0 \leq x(t) \leq C_2$ where $C_2 = \left(x_0 + \frac{K_3}{K_2}\right) e^{K_2(t_1-t_0)}$. ■

2.2 Necessary Conditions

In finding the optimal control, we first prove that there exists an optimal control. Then, using Pontryagin's Maximum Principle, we derive the necessary conditions that an optimal control and its corresponding states must satisfy. Lastly, we show that if a control is optimal, it is unique for sufficiently small t_1.

2.2.1 Existence of an Optimal Control

Here we prove that at least one optimal control exists that satisfies the optimal control formulation, Equations (2.1) - (2.4).

Theorem 2.2.1. *There exists an optimal control $u^* \in U$ which maximizes the objective functional $J(u)$.*

Proof: By Theorem 2.1.1, there exist constants $C_1, C_2 > 0$ such that $|x_n(t)| \leq C_2$ and $|y_n(t)| \leq C_1$ for all n and for all $t \in [t_0, t_1]$. Due to L^∞ bounds on the control and states,

$$\sup_{u \in U} J(u) < \infty.$$

Let $\{u_n(\cdot)\}_{n \geq 1}$ be a maximizing sequence, i.e.

$$\lim_{n \to \infty} J(u_n) = \max_{u \in U} J(u),$$

and x_n and y_n are the state trajectories corresponding to $u_n(\cdot)$. Since x_n and y_n are bounded for all n over $[t_0, t_1]$, x_n' and y_n' are bounded for all n over $[t_0, t_1]$. Thus, there exists $M_1, M_2 > 0$ such that $|x_n'(t)| \leq M_2$ and $|y_n'(t)| \leq M_1$. Let $M := \max\{M_1, M_2\}$, then $|x_n'(t)| \leq M$ and $|y_n'(t)| \leq M$ imply for all $t_\alpha, t_\beta \in [t_0, t_1]$

$$\begin{aligned} |x_n(t_\beta) - x_n(t_\alpha)| &\leq M\,|t_\beta - t_\alpha|\,, \quad \text{and} \\ |y_n(t_\beta) - y_n(t_\alpha)| &\leq M\,|t_\beta - t_\alpha|\,. \end{aligned}$$

Since both $x_n(t)$ and $y_n(t)$ are Lipschitz continuous with the same Lipschitz constant, M, $\{(x_n(t), y_n(t))\}$ is equicontinuous. Thus, by the Arzela-Ascoli Theorem, there exists $(x_n^*(t), y_n^*(t))$ such that

$$(x_n(t), y_n(t)) \to (x_n^*(t), y_n^*(t)) \text{ uniformly on } [t_0, t_1]\,.$$

For any n and t, $|u_n(t)| \leq 1$. Thus, $\{u_n(t)\}$ is uniformly bounded in L^∞ and therefore in L^2 on our finite time interval. Bounded sequences in L^2 have weakly convergent subsequences. Thus, there exists u^* such that

$$u_{n_k} \rightharpoonup u^* \text{ weakly in } L^2.$$

Using lower-semicontinuity of L^2 norms with respect to weak convergences,

$$\int_{t_0}^{t_1} (u^*)^2 \; dt \leq \liminf \int_{t_0}^{t_1} u_{n_k}^2 \; dt.$$

Since any subsequence must have the same limit as the sequence, we have

$$x^*(t_1) + By^*(t_1) - \int_{t_0}^{t_1} \left[A_1 \left(u^*\right)^2 (t) + A_2 u^*(t) \right] \; dt \;\geq\; \lim_{n \to \infty} J\left(u_n\right) \;=\; \max_{u \in U} J(u).$$

Using the convergences of the $\{x_n\}$ and $\{y_n\}$ sequences, we have that (x^*, y^*) are the states corresponding with the control u^*, and we obtain that

$$J(u^*) = \max_{u \in U} J(u).$$

■

2.2.2 Necessary Conditions and Characterization of an Optimal Control

Next, we use Pontryagin's Maximum Principle [33] to derive the characterization for an optimal control. Note, the following theorem assumes that there exists an optimal control, which is a valid assumption given Theorem 2.2.1.

Theorem 2.2.2. *Given an optimal control u^* and the solutions x^*, y^* of the corresponding state system (2.3)-(2.4) there exist adjoint variables λ_x and λ_y satisfying equations*

$$\begin{aligned}
\frac{d\lambda_x}{dt} &= r\lambda_x\left(3(x^*)^2 - 2(1+a)x^* + a\right), && (2.8)\\
\frac{d\lambda_y}{dt} &= s\lambda_y\left(3(y^*)^2 - 2(1+b)y^* + b\right) - p\lambda_x u^* + \lambda_y u^*, && (2.9)\\
\lambda_x(t_1) &= 1, && (2.10)\\
\lambda_y(t_1) &= B. && (2.11)
\end{aligned}$$

Furthermore, u^* is represented by

$$u^*(t) = \min\left\{1, \max\left\{0, \frac{-A_2 + \lambda_x(t)py^*(t) - \lambda_y(t)y^*(t)}{2A_1}\right\}\right\}. \tag{2.12}$$

Proof. Suppose u^* is an optimal control with corresponding states x^*, y^*. Using Pontryagin's Maximum Principle [33], the Hamiltonian is formed

$$\begin{aligned}
H &= -A_1u^2 - A_2u\\
&\quad - \lambda_x\left(r\left(x^3 - (a+1)x^2 + ax\right) - puy\right) - \lambda_y\left(s\left(y^3 - (b+1)y^2\right) + uy\right) && (2.13)
\end{aligned}$$

and we obtain the existence of adjoint functions satisfying

$$\begin{aligned}
\frac{d\lambda_x}{dt} &= -\frac{\partial H}{\partial x} = r\lambda_x\left(3(x^*)^2 - 2(1+a)x^* + a\right)\\
\frac{d\lambda_y}{dt} &= -\frac{\partial H}{\partial y} = s\lambda_y\left(3(y^*)^2 - 2(1+b)y^* + b\right) - p\lambda_x u^* + \lambda_y u^*,
\end{aligned}$$

and the transversality conditions, $\lambda_x(t_1) = 1$ and $\lambda_y(t_1) = B$.

The Hamiltonian differentiated with respect to the control gives

$$\frac{dH}{du} = -2A_1 - A_2 + \left[p\lambda_x(t) - \lambda_y(t)\right]y(t). \tag{2.14}$$

For the given objective functional, we maximize the Hamiltonian with respect to u.

When $\frac{\partial H}{\partial u} = 0$ at time t, then $0 \leq u^* \leq 1$.

$$\begin{aligned} \frac{\partial H}{\partial u} &= -2A_1 u - A_2 + \lambda_x p y - \lambda_y y = 0 \ \text{ at } \ u^*(t) \\ \Rightarrow \quad u^*(t) &= \frac{-A_2 + \lambda_x(t) p y^*(t) - \lambda_y(t) y^*(t)}{2A_1}. \end{aligned}$$

When $\frac{\partial H}{\partial u} < 0$ at t then $u^*(t) = 0$ and

$$-A_2 + \lambda_x p y^* - \lambda_y y^* < 0 \quad \Rightarrow \quad \frac{-A_2 + \lambda_x(t) p y^*(t) - \lambda_y(t) y^*(t)}{2A_1} < 0 = u^*(t).$$

When $\frac{\partial H}{\partial u} > 0$ at t then $u^*(t) = 1$ and

$$-A_2 + \lambda_x p y^* - \lambda_y y^* > 2A_1 \quad \Rightarrow \quad \frac{-A_2 + \lambda_x(t) p y^*(t) - \lambda_y(t) y^*(t)}{2A_1} > 1 = u^*(t).$$

Combining the cases above, we find a characterization of u^*:

$$u^*(t) = \min\left\{1, \max\left\{0, \frac{-A_2 + \lambda_x(t) p y^*(t) - \lambda_y(t) y^*(t)}{2A_1}\right\}\right\}. \tag{2.15}$$

■

2.2.3 Uniqueness of an Optimal Control for Small Final Time

The optimality system consists of the state system (Equations (2.3) and (2.4)) coupled with the adjoint system (Equations (2.8) - (2.11)) and the the optimal control characterization (Equation (2.15)). Thus, the following optimality system characterizes the optimal control

$$\begin{aligned} \frac{dx^*}{dt} &= r x^* (1 - x^*)(x^* - a) + p u^* y^*, && (2.16) \\ \frac{dy^*}{dt} &= s y^* (1 - y^*)(y^* - b) - u^* y^*, && (2.17) \\ \frac{d\lambda_x}{dt} &= r\lambda_x \left(3(x^*)^2 - 2(1+a)x^* + a\right), && (2.18) \\ \frac{d\lambda_y}{dt} &= s\lambda_y \left(3(y^*)^2 - 2(1+b)y^* + b\right) - p\lambda_x u^* + \lambda_y u^*, && (2.19) \\ u^*(t) &= \min\left\{1, \max\left\{0, \frac{-A_2 + \lambda_x(t) p y^*(t) - \lambda_y(t) y^*(t)}{2A_1}\right\}\right\}, && (2.20) \end{aligned}$$

with initial conditions $x^*(t_0) = x_0$ and $y^*(t_0) = y_0$, and transversality conditions $\lambda_x(t_1) = 1$ and $\lambda_y(t_1) = B$. Note here we use the star notation (x^*, y^*, and u^*) to indicate that the control and corresponding states are optimal. For the remainder of this section, we will drop the star notation for ease of reading.

We next prove that the solution of the optimality system (Equations (2.16)-(2.20)) is unique which gives the uniqueness of the optimal control. To do this, we first need the following lemma which derives the bounds on the adjoint functions.

Lemma 2.2.3. *Given the adjoint equations for λ_x and λ_y defined in Equations (2.8) and (2.9) there exist constants $C_3, C_4 > 0$ such that $0 < \lambda_x(t) \leq C_3$ and $0 \leq \lambda_y(t) \leq C_4$ for all $t \in [t_0, t_1]$.*

Proof. Given the adjoint equation for λ_x defined in Equation (2.8) with transversality condition $\lambda_x(t_1) = 1$,

$$\begin{aligned} \lambda_x' - r\lambda_x(3x^2 - 2(1+a)x + a) &= 0 \\ \frac{d}{d\sigma}\left(\lambda_x(\sigma)e^{\int_0^\sigma \left(3rx^2(\tau)-2r(1+a)x(\tau)+ar\right)\, d\tau}\right) &= 0. \end{aligned}$$

Integrating from t to t_1, we obtain

$$\lambda_x(t_1)e^{\int_0^{t_1}\left(3rx^2(\tau)-2r(1+a)x(\tau)+ar\right)\, d\tau} - \lambda_x(t)e^{\int_0^{t}\left(3rx^2(\tau)-2r(1+a)x(\tau)+ar\right)\, d\tau} = 0.$$

Solving for $\lambda_x(t)$, we obtain

$$\lambda_x(t) = e^{\int_t^{t_1}\left(3rx^2(\tau)-2r(1+a)x(\tau)+ar\right)\, d\tau} > 0.$$

By Theorem 2.1.1, $0 \leq x(t) \leq C_2$. Now, notice that

$$\begin{aligned} \lambda_x(t) &= e^{\int_t^{t_1}\left(3rx^2(\tau)-2r(1+a)x(\tau)+ar\right)\, d\tau} \\ &\leq e^{\int_t^{t_1}\left(3rC_2^2+ar\right)\, d\tau} \\ &= e^{(3rC_2^2+ar)(t_1-t)} \\ &\leq e^{(3rC_2^2+ar)t_1}, \end{aligned}$$

for all $t \in [t_0, t_1]$. Thus, we find that $0 < \lambda_x(t) \leq C_3$ for all $t \in [t_0, t_1]$ where $C_3 = e^{(3rC_2^2+ar)t_1}$.

Given the adjoint equation for λ_y defined in Equation (2.9) with transversality condition $\lambda_y(t_1) = B$,

$$\lambda_y' - \lambda_y(3sy^2 - 2s(1+b)y + bs + u) = -p\lambda_x u,$$

$$\frac{d}{d\sigma}\left(\lambda_y(\sigma)e^{\int_0^\sigma\left(3sy^2(\tau)-2s(1+b)y(\tau)+sb+u(\tau)\right)\, d\tau}\right) = -p\lambda_x(\sigma)u(\sigma)e^{\int_0^\sigma(3sy(\tau)-2s(1+b)y(\tau)+sb+u(\tau))\, d\tau}.$$

Integrating from t to t_1, we obtain,

$$\begin{aligned} &\lambda_y(t_1)e^{\int_0^{t_1}\left(3sy^2(\tau)-2s(1+b)y(\tau)+sb+u(\tau)\right)\, d\tau} - \lambda_y(t)e^{\int_0^{t}(3sy(\tau)-2s(1+b)y(\tau)+sb+u(\tau))\, d\tau} \\ &\quad = -p\int_t^{t_1}\lambda_x(\sigma)u(\sigma)e^{\int_0^\sigma(3sy(\tau)-2s(1+b)y(\tau)+sb+u(\tau))\, d\tau}\, d\sigma \end{aligned}$$

Solving for $\lambda_y(t)$, we obtain,

$$
\begin{aligned}
&\lambda_y(t)\\
&\quad = Be^{\int_t^{t_1}\left(3sy^2(\tau)-2s(1+b)y(\tau)+sb+u(\tau)\right)\, d\tau}\\
&\quad + pe^{-\int_0^t\left(3sy^2(\tau)-2s(1+b)y(\tau)+sb+u(\tau)\right)\, d\tau}\int_t^{t_1}\lambda_x(\sigma)u(\sigma)e^{\int_0^\sigma\left(3sy^2(\tau)-2s(1+b)y(\tau)+sb+u(\tau)\right)\, d\tau}\, d\sigma.
\end{aligned}
$$

Notice $\lambda_y(t) > 0$, since $B \geq 0$, $p \geq 0$, and $u(t) \geq 0$, $\lambda_x(t) > 0$ for all $t \in [t_0, t_1]$. Additionally, since $0 \leq u(t) \leq 1$, $0 < \lambda_x(t) \leq C_3$ for all $t \in [t_0, t_1]$,

$$
\begin{aligned}
\lambda_y(t) &\leq Be^{(3sC_1^2+sb+1)\int_t^{t_1}\, d\tau} + pC_3e^{2s(1+b)C_1\int_0^t\, d\tau}\int_t^{t_1} e^{(3sC_1^2+sb+1)\int_0^\sigma\, d\tau}\, d\sigma.\\
&\leq Be^{(3sC_1^2+sb+1)t_1} + pC_3e^{2s(1+b)C_1t_1}\int_t^{t_1} e^{(3sC_1^2+sb+1)\sigma}\, d\sigma\\
&= Be^{(3sC_1^2+sb+1)t_1} + \frac{pC_3e^{2s(1+b)C_1t_1}}{3sC_1^2+sb+1}e^{(3sC_1^2+sb+1)(t_1-t)}\\
&\leq Be^{(3sC_1^2+sb+1)t_1} + pC_3e^{(3sC_1^2+2s(1+b)C_1+sb+1)t_1}
\end{aligned}
$$

for $t \in [t_0, t_1]$ since $3sC_1^2 + sb + 1 > 1$. Thus, $0 \leq \lambda_y(t) \leq C_4$ for $t \in [t_0, t_1]$ where $C_4 = Be^{(3sC_1^2+sb+1)t_1} + pC_3e^{(3sC_1^2+2s(1+b)C_1+sb+1)t_1}$. ■

Now, using the bounds on the state equations and adjoint equations, we show that for sufficiently small t_1, the solution to the optimality system is unique.

Theorem 2.2.4. *For t_1 sufficiently small, the solution to the optimality system is unique.*

Proof. Suppose $(x, y, \lambda_x, \lambda_y)$ and $\left(\overline{x}, \overline{y}, \overline{\lambda_x}, \overline{\lambda_y}\right)$ are two solutions of the optimality system (Equations (2.16) - (2.20)). Let

$$
\begin{aligned}
x(t) &= e^{\alpha t}f(t) & \overline{x}(t) &= e^{\alpha t}\overline{f}(t)\\
y(t) &= e^{\alpha t}g(t) & \overline{y}(t) &= e^{\alpha t}\overline{g}(t)\\
\lambda_x(t) &= e^{-\alpha t}w(t) & \overline{\lambda_x}(t) &= e^{-\alpha t}\overline{w}(t)\\
\lambda_y(t) &= e^{-\alpha t}v(t) & \overline{\lambda_y}(t) &= e^{-\alpha t}\overline{v}(t)
\end{aligned}
$$

Using Theorems 2.2.1 and 2.2.2, the two solutions have the following characterizations of the optimal control

$$
\begin{aligned}
u^*(t) &= \min\left\{1, \max\left\{0, \frac{-A_2 + \lambda_x(t)py^*(t) - \lambda_y(t)y^*(t)}{2A_1}\right\}\right\}, \text{ and}\\
\overline{u}^*(t) &= \min\left\{1, \max\left\{0, \frac{-A_2 + \overline{\lambda_x}(t)p\overline{y}^*(t) - \overline{\lambda_y}(t)\overline{y}^*(t)}{2A_1}\right\}\right\}.
\end{aligned}
$$

Substituting $x = e^{\alpha t} f$, $y = e^{\alpha t} g$, $\lambda_x = e^{-\alpha t} w$, and $\lambda_y = e^{-\alpha t} v$ into Equations (2.16) - (2.19), the optimality system becomes

$$\begin{aligned}
\frac{dx}{dt} &= e^{\alpha t}\left(\frac{df}{dt} + \alpha f\right) = r e^{\alpha t} f \left(1 - e^{\alpha t} f\right)\left(e^{\alpha t} f - a\right) + p u e^{\alpha t} g && (2.21)\\
\frac{dy}{dt} &= e^{\alpha t}\left(\frac{dg}{dt} + \alpha g\right) = s e^{\alpha t} g \left(1 - e^{\alpha t} g\right)\left(e^{\alpha t} g - b\right) - u e^{\alpha t} g && (2.22)\\
\frac{d\lambda_x}{dt} &= e^{-\alpha t}\left(\frac{dw}{dt} - \alpha w\right) = r e^{-\alpha t} w \left(3(e^{\alpha t} f)^2 - 2(1+a) e^{\alpha t} f + a\right) && (2.23)\\
\frac{d\lambda_y}{dt} &= e^{-\alpha t}\left(\frac{dv}{dt} - \alpha v\right) = e^{-\alpha t}\left[s v \left(3(e^{\alpha t} g)^2 - 2(1+b) e^{\alpha t} g + b\right) + u(v - p w)\right] && (2.24)
\end{aligned}$$

with initial conditions $f(t_0) = e^{-\alpha t_0} x_0$ and $g(t_0) = e^{-\alpha t_0} y_0$, and transversality conditions $w(t_1) = e^{\alpha t_1}$ and $v(t_1) = B e^{\alpha t_1}$. We can construct a similar optimality system for the second solution $\left(\overline{x}, \overline{y}, \overline{\lambda_x}, \overline{\lambda_y}\right)$. Notice that

$$\begin{aligned}
x' - \overline{x}' &= e^{\alpha t}\left[\alpha(f - \overline{f}) + (f' - \overline{f}')\right] && (2.25)\\
y' - \overline{y}' &= e^{\alpha t}\left[\alpha(g - \overline{g}) + (g' - \overline{g}')\right] && (2.26)\\
-\left(\lambda_x' - \overline{\lambda_x}'\right) &= e^{-\alpha t}\left[\alpha(w - \overline{w}) - (w' - \overline{w}')\right] && (2.27)\\
-\left(\lambda_y' - \overline{\lambda_y}'\right) &= e^{-\alpha t}\left[\alpha(v - \overline{v}) - (v' - \overline{v}')\right]. && (2.28)
\end{aligned}$$

Using Equations (2.25)-(2.28) we construct the following equations

$$\begin{aligned}
\left(x' - \overline{x}'\right) \cdot e^{-\alpha t}\left(f - \overline{f}\right) &= \alpha\left(f - \overline{f}\right)^2 + \left(f' - \overline{f}'\right)\left(f - \overline{f}\right) && (2.29)\\
\left(y' - \overline{y}'\right) \cdot e^{-\alpha t}\left(g - \overline{g}\right) &= \alpha\left(g - \overline{g}\right)^2 + \left(g' - \overline{g}'\right)\left(g - \overline{g}\right) && (2.30)\\
-\left(\lambda_x' - \overline{\lambda_x}'\right) \cdot e^{\alpha t}\left(w - \overline{w}\right) &= \alpha\left(w - \overline{w}\right)^2 - \left(w' - \overline{w}'\right)\left(w - \overline{w}\right) && (2.31)\\
-\left(\lambda_y' - \overline{\lambda_y}'\right) \cdot e^{\alpha t}\left(v - \overline{v}\right) &= \alpha\left(v - \overline{v}\right)^2 - \left(v' - \overline{v}'\right)\left(v - \overline{v}\right) && (2.32)
\end{aligned}$$

Equation (2.29), for example, is formed by multiplying the difference $\left(\frac{dx}{dt} - \frac{d\bar{x}}{dt}\right)$ by $e^{-\alpha t}(f - \overline{f})$. Notice, using Equation (2.29) and the corresponding equation for $\overline{x}'$, the left hand side of Equation (2.29) can be rewritten as

$$\begin{aligned}
\left(x' - \overline{x}'\right) \cdot e^{-\alpha t}\left(f - \overline{f}\right) &= r(1+a) e^{\alpha t}(f + \overline{f})(f - \overline{f})^2 - r e^{2\alpha t}(f^3 - \overline{f}^3)(f - \overline{f})\\
&\quad - a r (f - \overline{f})^2 + p(ug - \overline{ug})(f - \overline{f})
\end{aligned}$$

The left hand sides of Equations (2.30) - (2.32) can each be rewritten in a similar fashion. Thus, we rewrite Equations (2.29) - (2.32) as

$$\begin{aligned}
\left(f' - \overline{f}'\right)\left(f - \overline{f}\right) + \alpha\left(f - \overline{f}\right)^2 &= r(1+a)e^{\alpha t}(f + \overline{f})(f - \overline{f})^2 - re^{2\alpha t}(f^3 - \overline{f}^3)(f - \overline{f}) \\
&\quad - ar(f - \overline{f})^2 + p(ug - \overline{ug})(f - \overline{f}) \qquad (2.33) \\
\left(g' - \overline{g}'\right)\left(g - \overline{g}\right) + \alpha\left(g - \overline{g}\right)^2 &= s(1+b)e^{\alpha t}(g + \overline{g})(g - \overline{g})^2 - se^{2\alpha t}(g^3 - \overline{g}^3)(g - \overline{g}) \\
&\quad - bs(g - \overline{g})^2 - (ug - \overline{ug})(g - \overline{g}) \qquad (2.34) \\
-\left(w' - \overline{w}'\right)\left(w - \overline{w}\right) + \alpha\left(w - \overline{w}\right)^2 &= -3re^{2\alpha t}(f^2 w - \overline{f}^2\overline{w})(w - \overline{w}) - ar(w - \overline{w})^2 \\
&\quad + 2r(1+a)e^{\alpha t}(fw - \overline{f}\overline{w})(w - \overline{w}) \qquad (2.35) \\
-\left(v' - \overline{v}'\right)\left(v - \overline{v}\right) + \alpha\left(v - \overline{v}\right)^2 &= -3se^{2\alpha t}(g^2 v - \overline{g}^2\overline{v})(v - \overline{v}) - bs(v - \overline{v})^2 \\
&\quad + 2s(1+b)e^{\alpha t}(gv - \overline{gv}) \\
&\quad - (uv - \overline{uv})(v - \overline{v}) + p(uw - \overline{uw})(v - \overline{v}) \qquad (2.36)
\end{aligned}$$

Next, Equations (2.33) - (2.36) are each integrated from t_0 to t_1.

$$\begin{aligned}
&\frac{1}{2}\left[f(t_1) - \overline{f}(t_1)\right]^2 + \alpha\int_{t_0}^{t_1}(f - \overline{f})^2\,dt = \\
&\quad r(1+a)\int_{t_0}^{t_1} e^{\alpha t}(f + \overline{f})(f - \overline{f})^2\,dt - r\int_{t_0}^{t_1} e^{2\alpha t}(f^3 - \overline{f}^3)(f - \overline{f})\,dt \\
&\quad - ar\int_{t_0}^{t_1}(f - \overline{f})^2\,dt + p\int_{t_0}^{t_1}(ug - \overline{ug})(f - \overline{f})\,dt \qquad (2.37)
\end{aligned}$$

$$\begin{aligned}
&\frac{1}{2}\left[g(t_1) - \overline{g}(t_1)\right]^2 + \alpha\int_{t_0}^{t_1}(g - \overline{g})^2\,dt = \\
&\quad s(1+b)\int_{t_0}^{t_1} e^{\alpha t}(g + \overline{g})(g - \overline{g})^2\,dt - s\int_{t_0}^{t_1} e^{2\alpha t}(g^3 - \overline{g}^3)(g - \overline{g})\,dt \\
&\quad - bs\int_{t_0}^{t_1}(g - \overline{g})^2\,dt - \int_{t_0}^{t_1}(ug - \overline{ug})(g - \overline{g})\,dt \qquad (2.38)
\end{aligned}$$

$$\begin{aligned}
&\frac{1}{2}\left[w(t_0) - \overline{w}(t_0)\right]^2 + \alpha\int_{t_0}^{t_1}(w - \overline{w})^2\,dt = \\
&\quad - 3r\int_{t_0}^{t_1} e^{2\alpha t}(f^2 w - \overline{f}^2\overline{w})(w - \overline{w})\,dt - ar\int_{t_0}^{t_1}(w - \overline{w})^2\,dt \\
&\quad + 2r(1+a)\int_{t_0}^{t_1} e^{\alpha t}(fw - \overline{f}\overline{w})(w - \overline{w})\,dt \qquad (2.39)
\end{aligned}$$

$$
\begin{aligned}
&\frac{1}{2}\left[v(t_0)-\overline{v}(t_0)\right]^2+\alpha\int_{t_0}^{t_1}(v-\overline{v})^2\,dt= \\
&\quad -3s\int_{t_0}^{t_1}e^{2\alpha t}(g^2v-\overline{g}^2\overline{v})(v-\overline{v})\,dt-bs\int_{t_0}^{t_1}(v-\overline{v})^2\,dt \\
&\quad +2s(1+b)\int_{t_0}^{t_1}e^{\alpha t}(gv-\overline{gv})(v-\overline{v})\,dt-\int_{t_0}^{t_1}(uv-\overline{uv})(v-\overline{v})\,dt \\
&\quad +p\int_{t_0}^{t_1}(uw-\overline{uw})(v-\overline{v})\,dt \qquad (2.40)
\end{aligned}
$$

Several terms in Equations (2.37)-(2.40) are estimated. The following terms are estimated using the upper bounds of the state equations found in Theorem 2.1.1. For several of the estimates we will use the fact that $1 \geq e^{-2\alpha t}$ for all $t \in [t_0, t_1]$ when $t_0 > 0$. The terms $\int_{t_0}^{t_1} e^{\alpha t}(f+\overline{f})(f-\overline{f})^2\,dt$ and $\int_{t_0}^{t_1} e^{\alpha t}(g+\overline{g})(g-\overline{g})^2\,dt$ in Equations (2.37) and (2.38) are estimated as

$$
\begin{aligned}
\int_{t_0}^{t_1} e^{\alpha t}(f+\overline{f})(f-\overline{f})^2\,dt \;&\leq\; \int_{t_0}^{t_1} e^{\alpha t}\left(2C_2e^{-\alpha t}\right)(f-\overline{f})^2\,dt \;\leq\; 2C_2\int_{t_0}^{t_1}(f-\overline{f})^2\,dt, \\
\int_{t_0}^{t_1} e^{\alpha t}(g+\overline{g})(g-\overline{g})^2\,dt \;&\leq\; \int_{t_0}^{t_1} e^{\alpha t}\left(2C_1e^{-\alpha t}\right)(g-\overline{g})^2\,dt \;\leq\; 2C_1\int_{t_0}^{t_1}(g-\overline{g})^2\,dt.
\end{aligned}
$$

The term $\int_{t_0}^{t_1} e^{2\alpha t}(f^3-\overline{f}^3)(f-\overline{f})\,dt$ in Equation (2.37) is estimated as

$$
\begin{aligned}
\int_{t_0}^{t_1} e^{2\alpha t}(f^3-\overline{f}^3)(f-\overline{f})\,dt \;&=\; \int_{t_0}^{t_1} e^{2\alpha t}(f-\overline{f})^2(f^2+f\overline{f}+\overline{f}^2)\,dt \\
&\leq\; \int_{t_0}^{t_1} e^{2\alpha t}(f-\overline{f})^2\left(3C_2^2e^{-2\alpha t}\right)\,dt \\
&=\; 3C_2^2\int_{t_0}^{t_1}(f-\overline{f})^2\,dt.
\end{aligned}
$$

Similarly, the term $\int_{t_0}^{t_1} e^{2\alpha t}(g^3-\overline{g}^3)(g-\overline{g})\,dt$ in Equation (2.38) is estimated as

$$
\int_{t_0}^{t_1} e^{2\alpha t}(g^3-\overline{g}^3)(g-\overline{g})\,dt \;\leq\; 3C_1^2\int_{t_0}^{t_1}(g-\overline{g})^2\,dt
$$

The term $\int_{t_0}^{t_1} e^{2\alpha t}(f^2 w - \overline{f}^2\overline{w})(w-\overline{w})\ dt$ in Equation (2.39) is estimated as

$$
\begin{aligned}
&\int_{t_0}^{t_1} e^{2\alpha t}(f^2 w - \overline{f}^2\overline{w})(w-\overline{w})\ dt \\
&\qquad = \int_{t_0}^{t_1} e^{2\alpha t}(f^2 w - f^2\overline{w} + f^2\overline{w} - \overline{f}^2\overline{w})(w-\overline{w})\ dt \\
&\qquad = \int_{t_0}^{t_1} e^{2\alpha t}\left[f^2(w-\overline{w})^2 + \overline{w}(f^2-\overline{f}^2)(w-\overline{w})\right]\ dt \\
&\qquad \le C_2^2\int_{t_0}^{t_1}(w-\overline{w})^2\ dt + C_3\int_{t_0}^{t_1} e^{3\alpha t}(f+\overline{f})(f-\overline{f})(w-\overline{w})\ dt \\
&\qquad \le C_2^2\int_{t_0}^{t_1}(w-\overline{w})^2\ dt + 2C_2C_3\int_{t_0}^{t_1} e^{2\alpha t}\left[(f-\overline{f})^2+(w-\overline{w})^2\right]\ dt \\
&\qquad \le \left(C_2^2 + 2C_2C_3e^{2\alpha t_1}\right)\int_{t_0}^{t_1}(w-\overline{w})^2\ dt + 2C_2C_3e^{2\alpha t_1}\int_{t_0}^{t_1}(f-\overline{f})^2\ dt.
\end{aligned}
$$

Similarly, the term $\int_{t_0}^{t_1} e^{2\alpha t}(g^2 v - \overline{g}^2\overline{v})(v-\overline{v})\ dt$ in Equation (2.40) is estimated as

$$
\int_{t_0}^{t_1} e^{2\alpha t}(g^2 v - \overline{g}^2\overline{v})(v-\overline{v})\ dt \le \left(C_1^2 + 2C_1C_4e^{2\alpha t_1}\right)\int_{t_0}^{t_1}(v-\overline{v})^2\ dt + 2C_1C_4e^{2\alpha t_1}\int_{t_0}^{t_1}(g-\overline{g})^2\ dt.
$$

The term $\int_{t_0}^{t_1} e^{\alpha t}(fw - \overline{f}\overline{w})(w-\overline{w})\ dt$ in Equation (2.39) is estimated as

$$
\begin{aligned}
&\int_{t_0}^{t_1} e^{\alpha t}(fw - \overline{f}\overline{w})(w-\overline{w}) \\
&\qquad = \int_{t_0}^{t_1} e^{\alpha t}(fw - f\overline{w} + f\overline{w} - \overline{f}\overline{w})(w-\overline{w})\ dt \\
&\qquad = \int_{t_0}^{t_1} e^{\alpha t}\left[f(w-\overline{w})^2 + \overline{w}(f-\overline{f})(w-\overline{w})\right]\ dt \\
&\qquad \le C_2\int_{t_0}^{t_1}(w-\overline{w})^2\ dt + C_3\int_{t_0}^{t_1} e^{2\alpha t}\left[(f-\overline{f})^2+(w-\overline{w})^2\right]^2\ dt \\
&\qquad \le \left(C_2 + C_3e^{2\alpha t_1}\right)\int_{t_0}^{t_1}(w-\overline{w})^2\ dt + C_3e^{2\alpha t_1}\int_{t_0}^{t_1}(f-\overline{f})^2\ dt.
\end{aligned}
$$

Similarly, the term $\int_{t_0}^{t_1} e^{\alpha t}(gv - \overline{gv})(v-\overline{v})\ dt$ in Equation (2.40) is estimated as

$$
\int_{t_0}^{t_1} e^{\alpha t}(gv - \overline{gv})(v-\overline{v})\ dt \le \left(C_1 + C_4e^{2\alpha t_1}\right)\int_{t_0}^{t_1}(v-\overline{v})^2\ dt + C_4e^{2\alpha t_1}\int_{t_0}^{t_1}(g-\overline{g})^2\ dt.
$$

Now, notice that

$$
\begin{aligned}
&\int_{t_0}^{t_1} (u-\overline{u})^2 \ dt \\
&\qquad \leq \frac{1}{4A_1^2} \int_{t_0}^{t_1} \left[pgw - gv - p\overline{gw} + \overline{gv}\right]^2 \ dt \\
&\qquad = \frac{1}{4A_1^2} \int_{t_0}^{t_1} \left[p(gw - \overline{gw}) - (gv - \overline{gv})\right]^2 \ dt \\
&\qquad \leq \frac{1}{2A_1^2} \int_{t_0}^{t_1} p^2(gw-\overline{gw})^2 + (gv-\overline{gv})^2 \ dt \\
&\qquad = \frac{p}{2A_1^2} \int_{t_0}^{t_1} \left[gw - g\overline{w} + g\overline{w} - \overline{gw}\right]^2 \ dt + \frac{1}{4A_1^2} \int_{t_0}^{t_1} \left[gv - g\overline{v} + g\overline{v} + \overline{gv}\right]^2 \ dt \\
&\qquad = \frac{p}{2A_1^2} \int_{t_0}^{t_1} \left[g(w-\overline{w}) + \overline{w}(g-\overline{g})\right]^2 \ dt + \frac{1}{4A_1^2} \int_{t_0}^{t_1} \left[g(v-\overline{v}) + \overline{v}(g-\overline{g})\right]^2 \ dt \\
&\qquad \leq \frac{p}{A_1^2} \int_{t_0}^{t_1} g^2(w-\overline{w})^2 + \overline{w}^2(g-\overline{g})^2 \ dt + \frac{1}{A_1^2} \int_{t_0}^{t_1} g^2(v-\overline{v})^2 + \overline{v}^2(g-\overline{g})^2 \ dt \\
&\qquad \leq \frac{(1+p^2)C_4^2 e^{2\alpha t_1}}{A_1^2} \int_{t_0}^{t_1} (g-\overline{g})^2 \ dt + \frac{p^2 C_1^2}{A_1^2} \int_{t_0}^{t_1} (w-\overline{w})^2 \ dt + \frac{C_1^2}{A_1^2} \int_{t_0}^{t_1} (v-\overline{v})^2.
\end{aligned}
$$

Let

$$
C_5 = \max\left\{1, \frac{p^2 C_1^2}{A_1^2}, \frac{C_1^2}{A_1^2}\right\}, \text{ and } C_6 = \max\left\{1, \frac{(1+p^2)C_4^2}{A_1^2}\right\}.
$$

Then

$$
\int_{t_0}^{t_1} (u-\overline{u})^2 \ dt \leq \left(C_5 + C_6 e^{2\alpha t_1}\right) \int_{t_0}^{t_1} \left[(g-\overline{g})^2 + (w-\overline{w})^2 + (v-\overline{v})^2\right] \ dt.
$$

Using the estimation for $\int_{t_0}^{t_1} (u-\overline{u})^2 \ dt$, the term $\int_{t_0}^{t_1} (ug-\overline{ug})(g-\overline{g}) \ dt$ in Equation (2.38) is estimated as

$$
\begin{aligned}
&\int_{t_0}^{t_1} (ug-\overline{ug})(g-\overline{g}) \ dt \\
&\qquad = \int_{t_0}^{t_1} (ug - u\overline{g} + u\overline{g} - \overline{ug})(g-\overline{g}) \ dt \\
&\qquad = \int_{t_0}^{t_1} u(g-\overline{g})^2 + \overline{g}(u-\overline{u})(g-\overline{g}) \ dt \\
&\qquad \leq \int_{t_0}^{t_1} u(g-\overline{g})^2 + \overline{g}(u-\overline{u})^2 + \overline{g}(g-\overline{g})^2 \ dt \\
&\qquad \leq \int_{t_0}^{t_1} (g-\overline{g})^2 \ dt + C_1 \int_{t_0}^{t_1} e^{-\alpha t}(u-\overline{u})^2 \ dt + C_1 \int_{t_0}^{t_1} e^{-\alpha t}(g-\overline{g})^2 \ dt.
\end{aligned}
$$

Continuing from the previous line

$$\begin{aligned}
&\int_{t_0}^{t_1} (ug-\overline{ug})(g-\overline{g})\ dt \\
&\quad\le \left(1+C_1e^{\alpha t_1}\right)\int_{t_0}^{t_1}(g-\overline{g})^2 + C_1e^{\alpha t_1}\int_{t_0}^{t_1}(u-\overline{u})^2\ dt \\
&\quad\le \left(1+C_1e^{\alpha t_1}\right)\int_{t_0}^{t_1}(g-\overline{g})^2 + C_1(C_5+C_6)e^{3\alpha t_1}\int_{t_0}^{t_1}(g-\overline{g})^2+(w-\overline{w})^2+(v-\overline{v})^2\ dt \\
&\quad\le \left(1+C_1(1+C_7)e^{3\alpha t_1}\right)\int_{t_0}^{t_1}(g-\overline{g})^2 + C_1C_7e^{3\alpha t_1}\int_{t_0}^{t_1}(w-\overline{w})^2+(v-\overline{v})^2\ dt,
\end{aligned}$$

where $C_7 = C_5 + C_6$. Similarly, the term $\int_{t_0}^{t_1}(uv-\overline{uv})(v-\overline{v})\ dt$ in Equation (2.40) is estimated as

$$\begin{aligned}
&\int_{t_0}^{t_1}(uv-\overline{uv})(v-\overline{v})\ dt \\
&\qquad\le \left(1+C_4(1+C_7)e^{3\alpha t_1}\right)\int_{t_0}^{t_1}(v-\overline{v})^2\ dt + C_4C_7e^{3\alpha t_1}\int_{t_0}^{t_1}(g-\overline{g})^2+(w-\overline{w})^2\ dt.
\end{aligned}$$

Using the estimation for $\int_{t_0}^{t_1}(u-\overline{u})^2\ dt$, the term $\int_{t_0}^{t_1}(ug-\overline{ug})(f-\overline{f})$ in Equation (2.37) is estimated as

$$\begin{aligned}
&\int_{t_0}^{t_1}(ug-\overline{ug})(f-\overline{f}) \\
&\quad= \int_{t_0}^{t_1}(ug-u\overline{g}+u\overline{g}-\overline{ug})(f-\overline{f})dt \\
&\quad= \int_{t_0}^{t_1}u(g-\overline{g})(f-\overline{f})+\overline{g}(u-\overline{u})(f-\overline{f})\ dt \\
&\quad\le \int_{t_0}^{t_1}\frac{1}{2}u\left[(g-\overline{g})^2+(f-\overline{f})^2\right]+\frac{1}{2}\overline{g}\left[(u-\overline{u})^2+(f-\overline{f})^2\right]\ dt \\
&\quad\le \frac{1}{2}\int_{t_0}^{t_1}(g-\overline{g})^2\ dt+\frac{1}{2}\left(1+C_1e^{\alpha t_1}\right)\int_{t_0}^{t_1}(f-\overline{f})^2\ dt+\frac{1}{2}C_1e^{\alpha t_1}\int_{t_0}^{t_1}(u-\overline{u})^2\ dt \\
&\quad\le \frac{1}{2}\int_{t_0}^{t_1}(g-\overline{g})^2\ dt+\frac{1}{2}\left(1+C_1e^{\alpha t_1}\right)\int_{t_0}^{t_1}(f-\overline{f})^2\ dt \\
&\qquad+\frac{1}{2}C_1e^{\alpha t_1}\left(C_5+C_6e^{2\alpha t_1}\right)\int_{t_0}^{t_1}\left[(g-\overline{g})^2+(w-\overline{w})^2+(v-\overline{v})^2\right]\ dt \\
&\quad\le \frac{1}{2}\left(1+C_1C_7e^{3\alpha t_1}\right)\int_{t_0}^{t_1}(g-\overline{g})^2\ dt+\frac{1}{2}\left(1+C_1e^{\alpha t_1}\right)\int_{t_0}^{t_1}(f-\overline{f})^2\ dt \\
&\qquad+\frac{1}{2}C_1C_7e^{3\alpha t_1}\int_{t_0}^{t_1}\left[(w-\overline{w})^2+(v-\overline{v})^2\right]\ dt
\end{aligned}$$

Similarly, the term $\int_{t_0}^{t_1}(uw - \overline{uw})(v-\overline{v})\ dt$ in Equation (2.40) is estimated as

$$\begin{aligned}\int_{t_0}^{t_1}(uw - \overline{uw})(v-\overline{v})\ dt &\leq \frac{1}{2}\left(1 + C_3C_7e^{3\alpha t_1}\right)\int_{t_0}^{t_1}(w-\overline{w})^2\ dt \\ &+ \frac{1}{2}\left(1 + C_3(1+C_7)e^{3\alpha t_1}\right)\int_{t_0}^{t_1}(v-\overline{v})^2\ dt + \frac{1}{2}C_3C_7e^{3\alpha t_1}\int_{t_0}^{t_1}(g-\overline{g})^2\ dt\end{aligned}$$

Next, we sum Equations (2.37) - (2.40) and use the estimates to form the following inequality

$$\begin{aligned}&\frac{1}{2}[f(t_1)-\overline{f}(t_1)]^2 + \frac{1}{2}[g(t_1)-\overline{g}(t_1)]^2 + \frac{1}{2}[w(t_0)-\overline{w}(t_0)]^2 + \frac{1}{2}[v(t_0)-\overline{v}(t_0)]^2 \\ &\quad + \alpha\int_{t_0}^{t_1}(f-\overline{f})^2 + (g-\overline{g})^2 + (w-\overline{w})^2 + (v-\overline{v})^2\ dt \\ &\leq \left(\tilde{C}_1 + \tilde{C}_2e^{3\alpha t_1}\right)\int_{t_0}^{t_1}\left[(f-\overline{f})^2 + (g-\overline{g})^2 + (w-\overline{w})^2 + (v-\overline{v})^2\right]\ dt,\end{aligned}$$

where $\tilde{C}_1$ and $\tilde{C}_2$ depend on the a, b, r, s, p, x_0, y_0 and the bounds of x, y, λ_x, and λ_y. If we rearrange the above inequality, we obtain,

$$\begin{aligned}&\left(\alpha - \tilde{C}_1 - \tilde{C}_2e^{3\alpha t_1}\right)\int_{t_0}^{t_1}\left[(f-\overline{f})^2 + (g-\overline{g})^2 + (w-\overline{w})^2 + (v-\overline{v})^2\right]\ dt \\ &\leq -\frac{1}{2}[f(t_1)-\overline{f}(t_1)]^2 - \frac{1}{2}[g(t_1)-\overline{g}(t_1)]^2 - \frac{1}{2}[w(t_0)-\overline{w}(t_0)]^2 - \frac{1}{2}[v(t_0)-\overline{v}(t_0)]^2 \\ &\leq 0.\end{aligned}$$

We choose α such that $\alpha > \tilde{C}_1 + \tilde{C}_2$. If

$$t_1 < \frac{1}{3\alpha}\ln\frac{\alpha - \tilde{C}_1}{\tilde{C}_2},$$

then $a - \tilde{C}_1 - \tilde{C}_2e^{3\alpha t_1} > 0$ and

$$\int_{t_0}^{t_1}\left[(f-\overline{f})^2 + (g-\overline{g})^2 + (w-\overline{w})^2 + (v-\overline{v})^2\right]\ dt \leq 0.$$

Thus,

$$\int_{t_0}^{t_1}\left[(f-\overline{f})^2 + (g-\overline{g})^2 + (w-\overline{w})^2 + (v-\overline{v})^2\right]\ dt = 0$$

and $f(t) = \overline{f}(t)$, $g(t) = \overline{g}(t)$, $w(t) = \overline{w}(t)$, and $v(t) = \overline{v}(t)$ for $t \in [t_0, t_1]$. Thus, for sufficiently small final time t_1, the solution to the optimality system is unique. ■

Remark 2.2.5. Since the optimal control and corresponding states and adjoints satisfy the optimality system, Equations (2.16) - (2.20), the optimal control is unique for sufficiently small t_1.

2.3 Numerical Methods

The optimal control can be numerically calculated under various parameter sets using a forward-backward sweep method [28] using 4^{th} order Runge-Kutta to solve the state equations (2.3) - (2.4) and their corresponding adjoint equations (2.8) - (2.9). The forward-backward sweep method makes an initial guess for u and then solves the state equations (2.3) - (2.4) forward in time using the Runge-Kutta method with the initial conditions (x_0 and y_0). Then, using the state values, the adjoint equations (2.8) - (2.9) are solved backwards in time using the Runge-Kutta method with the transversality conditions. At this point, the optimal control is updated using the characterization for the optimal control (2.12) and the values for the state and adjoint variables. This updated control replaces the initial control and the process is repeated until the successive iterates of control values are sufficiently close. The convergence of such an iterative method is based on the work of Hackbush [16]. Other examples using this method can be found in [12, 21, 37].

2.4 Numerical Results

In considering various parameter scenarios, the parameter constraints on x_0 and y_0, $x_0 < a$ and $y_0 > b$, must be included. For the examples here we take the minimum threshold for growth for both the target and reserve populations to be 0.3 (that is 30% of each populations' carrying capacity), and $x_0 = 0.25$ and $y_0 = 0.75$. Thus, the target population is starting just below its minimum threshold for growth and the reserve population is starting well above its minimum threshold for growth. Additionally, each scenario assumes that the intrinsic growth rate of the reserve population s is greater than the intrinsic growth rate of the target population r and in each scenario $r = 0.25$.

The results are divided into two sections. First, we show the numerical results for when $A_1 > 0$ and $A_2 = 0$. These results were published in [5]. The case where $A_1 = 0$ and $A_2 > 0$ is treated separately in Chapter 3.

2.4.1 Numerical Results for $A_2 = 0$

We first consider the impact of varying the cost of translocation, A_1. For the parameters listed in Figure 2.1 we vary the cost coefficient A_1 and show the resulting optimal control and states. Notice that for high cost $A_1 = 100$ (dashed line), the target population does not reach its minimum threshold for growth by the final time (i.e. $x(t_1) < a$). Thus, once augmentation has ceased (after the final time), the population will again start to decline. This illustrates the possibility of the cost of translocation being so high that, by the final time, the target population has not reached a density where it can sustain growth on its own. At the other extreme, with low cost coefficient $A_1 = 1$ (solid line), the target population exceeds its carrying capacity by the final time (i.e. $x(t_1) > 1$). Thus, the target population has been over-augmented, and once augmentation has ceased, the population will decline to its carrying capacity. In this case, resources would have been wasted in over-augmenting

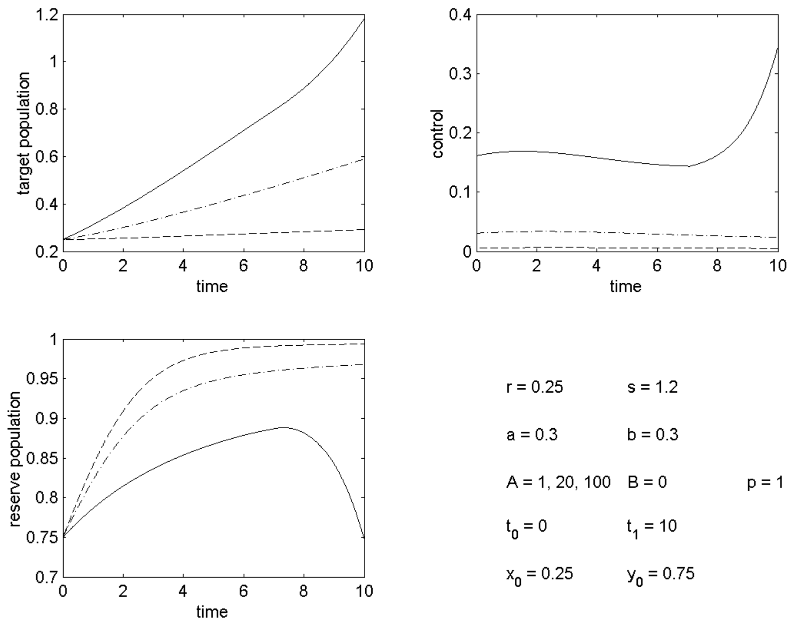


Figure 2.1: The target population, reserve population, and control when $A = 1, 20, 100$. The solid line corresponds to $A_1 = 1$, the dash-dot line to $A_1 = 20$, and the dashed line to $A_1 = 100$.

the target population. This "over-augmenting" arises from a limitation of the model; there is no constraint in the model that limits augmentation once the target population reaches carrying capacity. This may arise however in cases for which carrying capacity is not easily estimated and there are benefits to having larger target populations.

For the second scenario, the time horizon is varied, with t_1 being 5, 10, or 20. In Figure 2.2, notice that for each final time, the target population is above the minimum threshold for growth by the final time, though only by a small amount in the case of $t_1 = 5$. Additionally, for $t_1 = 20$, over the last five years of the augmentation $(15 < t < 20)$ the control increases again, and thus we see a slight decline in the density of the reserve population over those last five years.

In the third scenario, the ratio of the intrinsic growth rates of the target and reserve populations is varied by allowing the value of s to vary in $\{0.3, 0.9, 1.5\}$. For each value of s, Figure 2.3 shows that the target population is well above its minimum threshold for growth by the final time. When the value of s is higher, the reserve population is able to grow more quickly at the beginning of the time interval and achieve a higher population density by the end of the time interval. For $s = 0.3$, there is very little increase in the reserve population size over the entire time period. This is due to the fact that most of the growth in the reserve population is counter-balanced by the translocation of individuals to the target population.

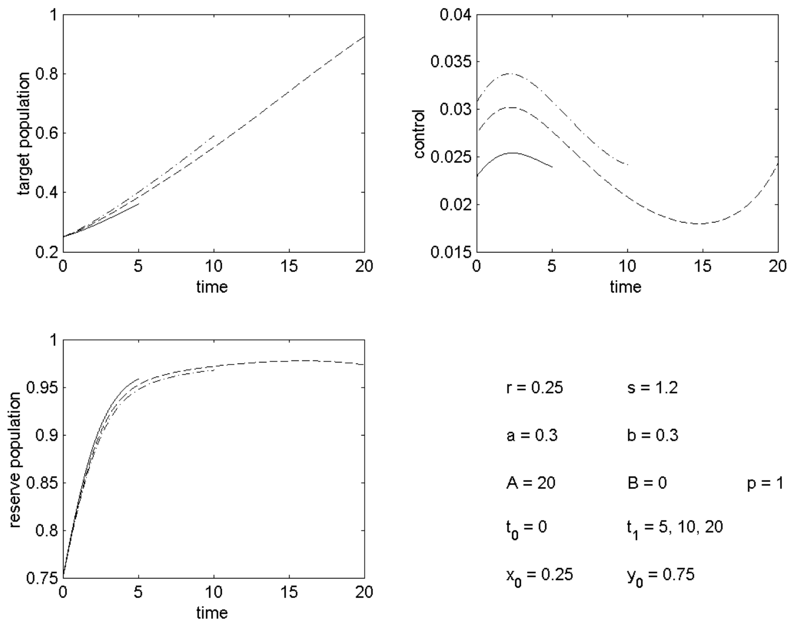


Figure 2.2: The target population, reserve population, and control when $t_1 = 5, 10, 20$. The solid line corresponds to $t_1 = 5$, the dash-dot line to $t_1 = 10$, and the dashed line to $t_1 = 20$.

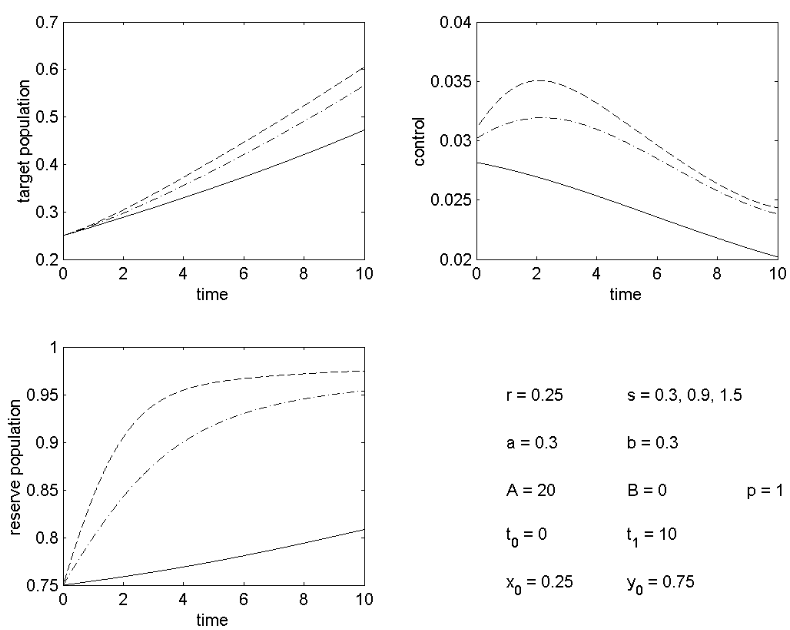


Figure 2.3: The target population, reserve population, and control when $s = 0.3, 0.9, 1.5$ and cost $A_1 = 20$. The solid line corresponds to $s = 0.3$, the dash-dot line to $s = 0.9$, and the dashed line to $s = 1.5$.

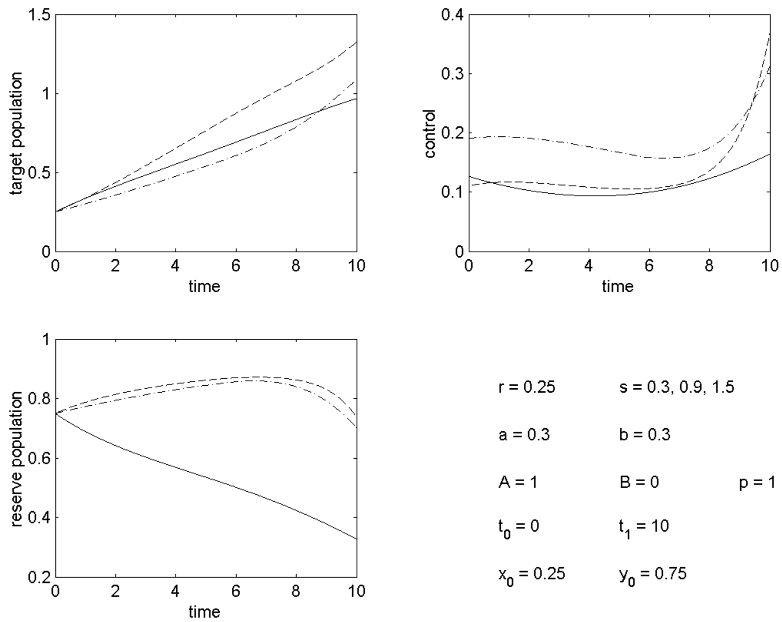


Figure 2.4: The target population, reserve population, and control when $s = 0.3, 0.9, 1.5$ and lower cost $A = 1$. The solid line corresponds to $s = 0.3$, the dash-dot line to $s = 0.9$, and the dashed line to $s = 1.5$.

In the fourth scenario all parameters are the same as in the third scenario with a lower cost of augmentation ($A_1 = 1$). Note in Figure 2.4, that by the final time, for $s = 0.9$ and $s = 1.5$, $x > 1$. Thus, the target population has been over-augmented. Also, notice that for $s = 0.3$ the reserve population is very close to its minimum threshold for growth by the final time. If the same scenario is run, except with $b = 0.4$, the results are quantitatively very similar, however the reserve population is below its minimum threshold for growth of $b = 0.4$. In this latter case, after the augmentation has taken place, the reserve population will decline to extinction. Thus, if the cost of augmentation is very low, it is possible that by the final time the reserve population has been "over-harvested," in that it will not naturally be able to increase its population density. This effect on the reserve population can be counteracted by increasing the value of B.

In prior scenarios the value of B has been set to zero, which means the objective function is not affected by the size of the reserve population at the final time. It may be necessary to increase B in order to prevent the reserve population from falling below its minimum threshold for growth by the final time. In the fifth scenario, $B = 0.75$ (all other parameter values are the same as in the fourth scenario). Thus, it is 75% as important to maximize the reserve population at the final time as it is to maximize the target population by the final time. In Figure 2.5 notice that the reserve population, for each value of s, is now well above the minimum threshold for growth, as is expected when increasing the value of B.

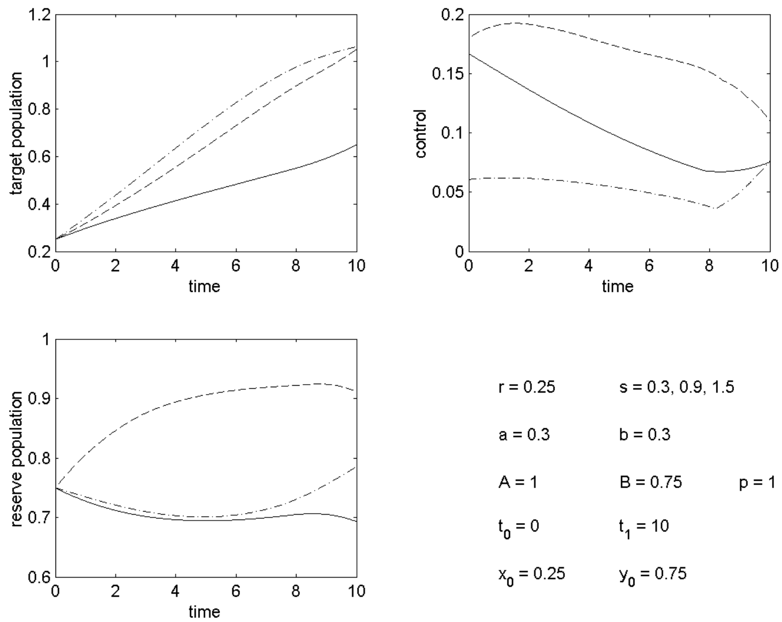


Figure 2.5: The target population, reserve population, and control when $s = 0.3, 0.9, 1.5$, cost $A_1 = 1$, and $B = 0.75$. The solid line corresponds to $s = 0.3$, the dash-dot line to $s = 0.9$, and the dashed line to $s = 1.5$.

Also notice that the target population, for $s = 0.9$ and $s = 1.5$, is still above a density of 1 by the final time, so there is still over-augmenting.

Figure 2.6 shows the effect of changing the ratio of the carrying capacities, p. Notice for $p = 0.1$ virtually no augmentation takes place, and that $x(t_1) < a$, so the target population will decline again after augmentation is completed. This means that when the carrying capacity of the reserve population is only 10% of the carrying capacity of the target population there are not enough individuals in the reserve population to effectively augment the target population (i.e., have $x(t_1) > a$). However, further numerical simulations show that for all other parameter values remaining the same, a value of $p > 0.2$ was sufficient to guarantee that $x(t_1) > a$. Thus, it is possible to have a reserve population with a much smaller carrying capacity and still have effective augmentation of the target population. Notice also that when $p = 0.7$ the target population is over-augmented. In this scenario the cost of augmentation A_1 was set to a low value of 1. If the cost of augmentation is raised, larger and larger values of p are needed to ensure $x(t_1) > a$. For example, with all other values remaining the same, if $A_1 = 20$, a value of $p > 0.48$ is needed to guarantee that $x(t_1) > a$, and if $A_1 = 100$, a value of $p > 1.05$ is needed to guarantee that $x(t_1) > a$.

The sets of results described above by no means exhaust the possible sets of scenarios that could be shown. However, numerous scenarios covering the breath of the biologically feasible parameter space were conducted, and the results shown above display the gamut of dynamical results collected from all the scenarios tested.

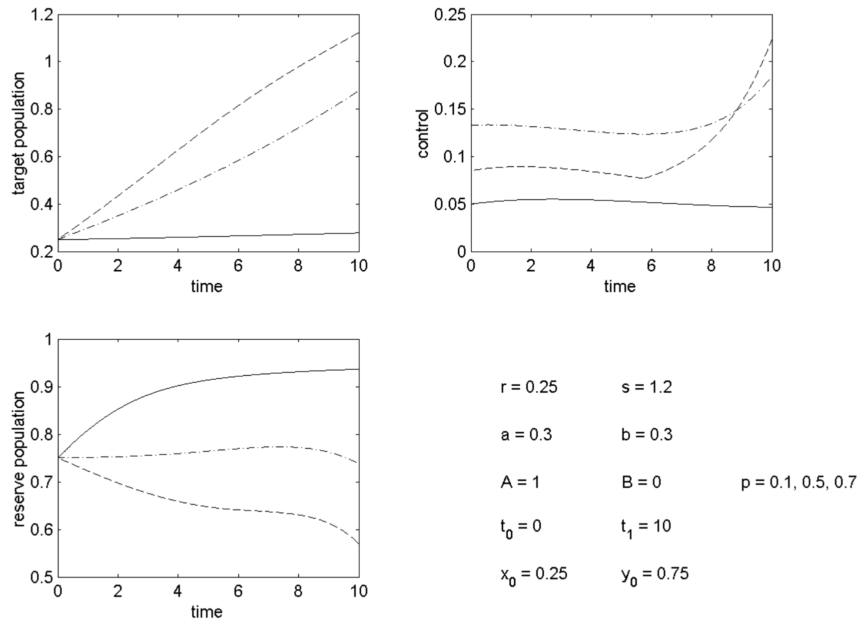


Figure 2.6: The target population, reserve population, and control when $p = 0.1, 0.5, 0.7$. The solid line corresponds to $p = 0.1$, the dash-dot line to $p = 0.5$, and the dashed line to $p = 0.7$.

2.5 Conclusions

Several important conclusions about the continuous control of species augmentation can be drawn from this model. First, high cost of augmentation can prevent moving sufficient numbers of individuals to the target population in order for the target population to be above its minimum threshold for growth by the final time. Additionally, a low p value can exacerbate this effect; having a lower ratio of the carrying capacity of the reserve to the target population necessitates having a lower cost in order to optimally augment the target population such that it is above its minimum threshold for growth by the final time. If, in fact, the target population does not reach its minimum threshold for growth by the final time, then additional future augmentations may be required to prevent the population from going extinct. Additionally, the combination of a low cost of translocation and a low intrinsic growth rate of the reserve population could cause the reserve population to fall below its threshold for population growth by the final time. However, this can be counteracted in the optimal control solution by increasing the importance of having a large reserve population by the final time (i.e., increase the value of B). All of the above conclusions conform to intuition. However, our results provide considerably more detail about the exact dynamics of optimal augmentation than can be readily intuited.

One of the drawbacks of this model is that it does not provide a constraint to prevent over-augmenting the target population. In Figures 2.4, 2.5, and 2.6, we see that it is possible for the optimal augmentation strategy to continue augmenting the target population even after its density has increased past 1, i.e., above its carrying capacity. Once the augmentation is complete the target population will fall back down to its carrying capacity and remain there. Thus, over-augmenting is not cost effective as it requires the translocation of "extra" individuals from the reserve population. Possible modifications to prevent excess cost due to over-augmenting include stopping augmentation once the target population has been over augmented (i.e. $u(t) = 0$ when $x(t) \geq 1$), or placing a final time condition on the target population (i.e. $x(t_1) = 1 - \delta$ where $0 \leq \delta << 1$).

Our model places no restriction on what proportion of the reserve population can be translocated to the target population. However, it may be unreasonable to allow all the individuals in the reserve population to be moved. Thus, another reasonable modification is to consider a constraint that ensures the reserve population will be above its minimum threshold for growth by the final time, i.e. $y(t_1) \leq b$, or will be maintained above this throughout the entire period. Our model was for control in continuous time of species augmentation. However, in practice, species augmentation often happens in a discrete manner, moving individuals to the target population at discrete times. A discrete-time formulation of optimal augmentation presents somewhat different mathematical challenges, in part due to the fact that there are constraints associated with the time scale of allowed augmentation that may not match with the time scales of population growth (typically annual for many mammal species). We are unaware of any comparisons of continuous versus discrete time optimal control applied in a population management context, and the introduction of discrete-time may well lead to complex underlying model behavior as occurs for example in the discrete logistic model.

Associated with optimal augmentation strategies are the numerous issues which arise from introduction of more detailed assumptions about the underlying populations. Conclusions about population behavior may be quite different when complications such as population demographic structure and genetics are incorporated. We expect that expansion to include these aspects of population structure, though leading to quantitative population analyses that may be more readily applicable, would no doubt lead to more complex optimal strategies that may not be readily feasible (there would be controls associated with each population age class for example). So additional feasibility constraints might have to be placed on the control space. A quite different set of models would be necessary if the community-level aspects of augmentation strategies were to be considered. Optimal augmentation following our above results may be singularly unsuccessful if the augmented population were prey for a predator population with density-dependent impacts on the prey. This could arise for example if, once augmented, the prey population was in sufficiently high density as to lead to predator switching, perhaps due to an enhanced search image of the predator for this prey species now occurring at higher density. Similar problems may arise if the augmented population was the predator in the system, or if competitive interactions were involved. Thus, the work presented here is simply a first-step toward building a general theory of population augmentation which accounts for the complexities inherent in many conservation biology applications. One challenge in developing this theory is to account for the practical constraints faced by natural system managers in carrying out augmentation.

Chapter 3

Continuous Time Model with Linear Objective Functional

In this chapter we consider the same optimal control formulation as in Chapter 2, except that we assume the cost term in the objective functional to be linear with respect to the control variable. Otherwise, the assumptions of the formulation remain the same. We demonstrate the effects of a linear objective functional on the optimal control and corresponding states.

We assume the objective of augmentation is to maximize the target population at a given final time while minimizing the cost. This assumes there is cost associated with translocating an individual from the reserve population. We assume this cost to be a linear function of the fraction translocated, so we have the quadratic cost coefficient $A_1 = 0$. We assume that the total population $(x + y)$ is to be maximized at the final time, with different relative weights applied to the reserve and target populations. We assume it is not as important to maximize the reserve population as it is the target population by the final time. Additionally, we assume that the target population x has an initial density x_0 below its minimum threshold for growth $0 < a < 1$, and that the reserve population y has an initial density y_0 above its minimum threshold for growth $0 < b < 1$. Thus, $x_0 < a$ and $y_0 > b$.

Thus, the optimal control formulation is

$$\max_{u \in U} \left[x(t_1) + By(t_1) - \int_{t_0}^{t_1} A_2 u(t)\ dt \right] \tag{3.1}$$

where

$$U = \{u : [t_0, t_1] \to [0, 1] \mid u \text{ Lebesgue measurable}\} \tag{3.2}$$

and

$$x'(t) = rx(1-x)(x-a) + puy, \quad x(t_0) = x_0 \text{ where } 0 < x_0 < a < 1 \tag{3.3}$$

$$y'(t) = sy(1-y)(y-b) - uy, \quad y(t_0) = y_0 \text{ where } 0 < b < y_0 < 1 \tag{3.4}$$

and a, b, t_0, t_1, x_0, y_0, r, s, A_2, and B are all non-negative constants, with $0 \leq B \leq 1$. The objective functional seeks to maximize the two populations at the final time while minimizing the cost associated with translocating an individual from the reserve population to the target population. Here the cost is linear in the control. The weight factor B balances out the relative importance of maximizing the reserve population. We assume x_0 and y_0 are positive. Within this formulation, we see to find the control u^* that maximizes the objective functional

$$J(u) = x(t_1) + By(t_1) - \int_{t_0}^{t_1} A_2 u(t)\, dt. \tag{3.5}$$

In the remainder of this chapter we derive the necessary conditions that the optimal control and corresponding states must satisfy (Section 3.1), determine a characterization of the optimal control (Theorem 3.1.1), discuss the appropriate numerical method used to investigate a specific parameter scenario (Section 3.2), explore the numerical results of several different illustrative parameter scenarios (Section 3.3), and finally discuss the conclusions that can be made from the illustrative parameter scenarios (Section 3.4).

3.1 Necessary Conditions

Next, we use Pontryagin's Maximum Principle [33] along with the generalized Legendre-Clebsch Condition [9, 26] to derive the necessary conditions that an optimal control and its corresponding states must satisfy. The following theorem assumes that there exists an optimal control. Since Theorems 2.1.1 and 2.2.1 do not depend on the positivity of A_1, we have that there exists an optimal control $u^* \in U$ which maximizes the objective function $J(u)$ given in Equation (3.5).

3.1.1 Necessary Conditions and Characterization of an Optimal Control

In the case of the quadratic objective functional (see Chapter 2), one can find an explicit formula to characterize the optimal control in terms of the state and adjoint variables. However, in this case, we note that the optimal control characterization is different and there is a possibility of bang-bang and singular controls.

Theorem 3.1.1. *Given an optimal control u^* and the corresponding solutions to the state system given in equations (3.3)-(3.4), there exist adjoint variables λ_x and λ_y satisfying equations*

$$\begin{aligned}
\frac{d\lambda_x}{dt} &= r\lambda_x \left(3(x^*)^2 - 2(1+a)x^* + a\right), & (3.6)\\
\frac{d\lambda_y}{dt} &= s\lambda_y \left(3(y^*)^2 - 2(1+b)y^* + b\right) - p\lambda_x u^* + \lambda_y u^*, & (3.7)\\
\lambda_x(t_1) &= 1, & (3.8)\\
\lambda_y(t_1) &= B. & (3.9)
\end{aligned}$$

Furthermore, u^* is characterized by

$$u^*(t) = \begin{cases} 0 & \text{if} \quad \psi(t) < 0 \\ 1 & \text{if} \quad \psi(t) > 0 \end{cases} \tag{3.10}$$

where

$$\psi(t) = -A_2 + [p\lambda_x(t) - \lambda_y(t)]\, y(t). \tag{3.11}$$

Let

$$\begin{aligned} F(x, y, &\lambda_x, \lambda_y) = \\ &pr\lambda_x' \left[3x^2 - 2(1+a)x + a\right] - 2pr^2\lambda_x xy\,[3x - 1 - a]\left[x^2 - (1+a)x + a\right] \\ &- s^2\lambda_y y^2 \left[3y^2 - 2(1+b)y + b\right][2y - 1 - b] \\ &- sy\left[y^2 - (1+b)y + b\right]\left[2p\lambda_x' - 4\lambda_y y\,(3y - 1 - b) - ps\lambda_x\left(3y^2 - 2(1+b)y + b\right)\right], \end{aligned} \tag{3.12}$$

and

$$\begin{aligned} G(x, y, &\lambda_x, \lambda_y) = \\ &p^2 r\lambda_x y^2 - pr\lambda_x y\left[3x^2 - 2(1+a)x + a\right] + ps\lambda_x y\left(5y^2 - 3(1+b)y + b\right) \\ &+ s\lambda_y y^2\,(4y - 1 - b)\,. \end{aligned} \tag{3.13}$$

If $\psi(t) = 0$ on a non-empty open interval $(t_\alpha, t_\beta) \subset (t_0, t_1)$, then the singular control

$$u_s(t) = -\frac{F(x, y, \lambda_x, \lambda_y)}{G(x, y, \lambda_x, \lambda_y)} \tag{3.14}$$

is optimal on $[t_\alpha, t_\beta]$ if the inequalities

$$G(x, y, \lambda_x, \lambda_y) > 0 \ \text{and} \ \ 0 \le -\frac{F(x, y, \lambda_x, \lambda_y)}{G(x, y, \lambda_x, \lambda_y)} \le 1 \tag{3.15}$$

hold on the interval $[t_\alpha, t_\beta]$.

Proof. Suppose u^* is an optimal control with corresponding states x^*, y^*. Using Pontryagin's Maximum Principle, the Hamiltonian is formed

$$H = -A_2 u + \lambda_x\left(rx(1-x)(x-a) + puy\right) + \lambda_y\left(sy(1-y)(y-b) - uy\right) \tag{3.16}$$

and the adjoint equations are the same as in Equations (2.8) and (2.9) with the same transversality conditions as in Equations (2.10) and (2.11). Define $\psi(t)$ as the coefficient of u in the Hamiltonian

$$\psi(t) = \frac{\partial H}{\partial u} = -A_2 + [p\lambda_x(t) - \lambda_y(t)]\, y(t)$$

and we call $\psi(t)$ the *switching function*. In this case, if we maximize the Hamiltonian with respect to u, the characterization of the optimal control at time t is

$$u^*(t) = \begin{cases} 0 & \text{if} \quad \psi < 0 \\ 1 & \text{if} \quad \psi > 0. \end{cases}$$

We investigate the case where $\psi = 0$, i.e. the case of the singular control. Let u_s denote the singular control. Thus, for times in $[t_0, t_1]$ where $\psi \neq 0$ we have a bang-bang control, meaning the optimal control takes values at its lower or upper bounds. When the switching function is zero on a non-trivial interval, we have the singular case. In order to determine whether u_s, is optimal over the non-trivial interval, we check the generalized Legendre-Clebsch condition.

The generalized Legendre-Clebsch Condition [9, 26] states that if the singular control is maximizing on the interval $[t_\alpha, t_\beta]$ then

$$(-1)^q \, \frac{\partial}{\partial u} \, \frac{d^{2q}}{dt^{2q}} \, \psi(t) \leq 0,$$

where q is the least integer such that

$$\frac{\partial}{\partial u} \, \frac{d^{2q}}{dt^{2q}} \, \psi(t) \neq 0.$$

To find u_s and to form this condition, we take the first time derivative of the switching function,

$$\psi'(t) = \left[p\lambda_x' - \lambda_y'\right] y + \left[p\lambda_x - \lambda_y\right] y' \tag{3.18}$$

where $\psi'(t) = \dfrac{d\psi}{dt}$, $\lambda_x' = \dfrac{d\lambda_x}{dt}$, $\lambda_y' = \dfrac{d\lambda_y}{dt}$, and $y' = \dfrac{dy}{dt}$. Since λ_x' contains no u terms, we leave λ_x' as the notation in Equation (3.18) instead of replacing it with the right hand side of the differential equation as is done for λ_y' and y',

$$\begin{aligned} \psi'(t) \quad = \quad & p\lambda_x' y - s\lambda_y \left[3y^3 - 2(1+b)y^2 + by\right] + p\lambda_x u y - \lambda_y u y \\ & -ps\lambda_x \left[y^3 - (1+b)y^2 + by\right] - p\lambda_x u y + s\lambda_y \left[y^3 - (1+b)y^2 + by\right] + \lambda_y u y \end{aligned}$$

The terms with the control u cancel each other out, leaving no u terms in this first derivative. Simplifying,

$$\psi'(t) = p\lambda_x' y - ps\lambda_x \left[y^3 - (1+b)y^2 + by\right] - s\lambda_y \left[2y^3 - (1+b)y^2\right]. \tag{3.19}$$

Next, take the second time derivative of the switching function,

$$\begin{aligned}
\psi''(t) &= p\lambda_x''y + p\lambda_x'y' - ps\lambda_x'\left[y^3 - (1+b)y^2 + by\right] - ps\lambda_x\left[3y^2 - 2(1+b)y + b\right]y' \\
&\quad - s\lambda_y'\left[2y^3 - (1+b)y^2\right] - s\lambda_y\left[6y^2 - 2(1+b)y\right]y' \\
\\
&= p\lambda_x''y - ps\lambda_x'\left[y^3 - (1+b)y^2 + by\right] - s\lambda_y'\left[2y^3 - (1+b)y^2\right] \\
&\quad + y'\left[p\lambda_x' - 6s\lambda_y y^2 + 2(1+b)s\lambda_y y - 3ps\lambda_x y^2 + 2p(1+b)s\lambda_x y - pbs\lambda_x\right]
\end{aligned}$$

Note that λ_x'' is

$$\lambda_x'' = r\lambda_x'\left[3x^2 - 2(1+a)x + a\right] - r^2\lambda_x\left[6x - 2(1+a)\right]\left[x^3 - (1+a)x^2 + ax\right] + pr\lambda_x uy.$$

Substitute in the right hand sides of y', λ_y', and λ_x''. Again, since λ_x' has no dependence on u, we need not substitute in the right hand side of its equation,

$$\begin{aligned}
\psi''(t) &= pr\lambda_x'y\left[3x^2 - 2(1+a)x + a\right] - pr^2\lambda_x y\left[6x - 2(1+a)\right]\left[x^3 - (1+a)x^2 + ax\right] \\
&\quad + p^2r\lambda_x uy^2 - ps\lambda_x'\left[y^3 - (1+b)y^2 + by\right] \\
&\quad - s\left[s\lambda_y\left(3y^2 - 2(1+b)y + b\right) - p\lambda_x u + \lambda_y u\right]\left[2y^3 - (1+b)y^2\right] \\
&\quad + \left[s\left(-y^3 + (1+b)y^2 - by\right) - uy\right]\left[p\lambda_x' - 6s\lambda_y y^2 + 2(1+b)s\lambda_y y - 3ps\lambda_x y^2\right. \\
&\qquad \left. + 2p(1+b)s\lambda_x y - pbs\lambda_x\right].
\end{aligned}$$

Lastly, we collect all the u terms together and then combine like u terms.

$$\begin{aligned}
\psi''(t) &= pr\lambda_x' \left[3x^2 - 2(1+a)x + a\right] - 2pr^2\lambda_x xy\,[3x-1-a]\left[x^2-(1+a)x+a\right] \\
&\quad -s^2\lambda_y y^2\left[3y^2-2(1+b)y+b\right][2y-1-b] \\
&\quad -sy\left[y^2-(1+b)y+b\right]\left[2p\lambda_x' - 4\lambda_y y\,(3y-1-b) - ps\lambda_x\left(3y^2-2(1+b)y+b\right)\right] \\
&\quad +u\left[p^2r\lambda_x y^2 + 2ps\lambda_x y^3 - p(1+b)s\lambda_x y^2 - 2s\lambda_y y^3 + (1+b)s\lambda_y y^2 - p\lambda_x' y\right. \\
&\qquad\quad \left. +6s\lambda_y y^3 - 2(1+b)s\lambda_y y^2 + 3ps\lambda_x y^3 - 2p(1+b)s\lambda_x y^2 + pbs\lambda_x y\right] \\
&= pr\lambda_x' \left[3x^2 - 2(1+a)x + a\right] - 2pr^2\lambda_x xy\,[3x-1-a]\left[x^2-(1+a)x+a\right] \\
&\quad -s^2\lambda_y y^2\left[3y^2-2(1+b)y+b\right][2y-1-b] \\
&\quad -sy\left[y^2-(1+b)y+b\right]\left[2p\lambda_x' - 4\lambda_y y\,(3y-1-b) - ps\lambda_x\left(3y^2-2(1+b)y+b\right)\right] \\
&\quad +u\left[p^2r\lambda_x y^2 + 5ps\lambda_x y^3 - 3p(1+b)s\lambda_x y^2 + pbs\lambda_x y\right. \\
&\qquad\quad \left. 4s\lambda_y y^3 - s(1+b)\lambda_y y^2 - p\lambda_x' y\right]
\end{aligned}$$

$$\begin{aligned}
\psi''(t) &= pr\lambda_x' \left[3x^2 - 2(1+a)x + a\right] - 2pr^2\lambda_x xy\,[3x-1-a]\left[x^2-(1+a)x+a\right] \\
&\quad -s^2\lambda_y y^2\left[3y^2-2(1+b)y+b\right][2y-1-b] \\
&\quad -sy\left[y^2-(1+b)y+b\right]\left[2p\lambda_x' - 4\lambda_y y\,(3y-1-b) - ps\lambda_x\left(3y^2-2(1+b)y+b\right)\right] \\
&\quad +u\left[p^2r\lambda_x y^2 - p\lambda_x' y + ps\lambda_x y\left(5y^2-3(1+b)y+b\right) + s\lambda_y y^2\,(4y-1-b)\right].
\end{aligned}$$

Since this second time derivative has u terms, we have

$$\frac{\partial}{\partial u}\frac{d^2}{dt^2}\psi(t) \neq 0$$

on the interval $[t_\alpha, t_\beta]$. So we take the partial derivative with respect to u of $\dfrac{d^2\psi}{dt^2}$

$$\frac{\partial}{\partial u}\,\frac{d^2\psi}{dt^2} = p^2r\lambda_x y^2 - p\lambda_x' y + ps\lambda_x y\left(5y^2-3(1+b)y+b\right) + s\lambda_y y^2\,(4y-1-b)$$

Substitute in the right hand side of λ_x' to get

$$\begin{aligned}
\frac{\partial}{\partial u}\,\frac{d^2\psi}{dt^2} &= p^2r\lambda_x y^2 - pr\lambda_x y\left[3x^2-2(1+a)x+a\right] + ps\lambda_x y\left(5y^2-3(1+b)y+b\right) \\
&\quad + s\lambda_y y^2\,(4y-1-b)
\end{aligned} \tag{3.20}$$

The generalized Legendre-Clebsch Condition tells us that the singular control is maximizing when

$$\begin{aligned}
p^2r\lambda_x y^2 - pr\lambda_x y\left[3x^2-2(1+a)x+a\right] + ps\lambda_x y\left(5y^2-3(1+b)y+b\right)& \\
+ s\lambda_y y^2\,(4y-1-b) &\geq 0.
\end{aligned} \tag{3.21}$$

Notice the left hand side of inequality (3.21) is $\dfrac{\partial}{\partial u}\dfrac{d^2\psi}{dt^2}$. We can derive an equation for the singular control u_s by solving $\psi''(t) = 0$ for u. If we do this, we get

$$u_s = -\frac{F(x, y, \lambda_x, \lambda_y)}{G(x, y, \lambda_x, \lambda_y)}$$

where u_s is the singular solution, and

$$\begin{aligned}
F(x, y,&\lambda_x, \lambda_y) = \\
&pr\lambda_x' \left[3x^2 - 2(1+a)x + a\right] - 2pr^2\lambda_x xy \left[3x - 1 - a\right] \left[x^2 - (1+a)x + a\right] \\
&- s^2\lambda_y y^2 \left[3y^2 - 2(1+b)y + b\right] \left[2y - 1 - b\right] \\
&- sy \left[y^2 - (1+b)y + b\right] \left[2p\lambda_x' - 4\lambda_y y \left(3y - 1 - b\right) - ps\lambda_x \left(3y^2 - 2(1+b)y + b\right)\right],
\end{aligned} \tag{3.22}$$

and

$$\begin{aligned}
G(x, y,&\lambda_x, \lambda_y) = \\
&p^2 r\lambda_x y^2 - pr\lambda_x y \left[3x^2 - 2(1+a)x + a\right] + ps\lambda_x y \left(5y^2 - 3(1+b)y + b\right) \\
&+ s\lambda_y y^2 \left(4y - 1 - b\right)
\end{aligned} \tag{3.23}$$

Substituting the right hand sides of λ_x' and λ_x'' into Equation (3.22) yields

$$\begin{aligned}
F \;=\; & pr^2\lambda_x \left[3x^2 - 2(1+a)x + a\right]^2 - 2pr^2\lambda_x xy \left[3x - 1 - a\right] \left[x^2 - (1+a)x + a\right] \\
& -s^2\lambda_y y^2 \left[3y^2 - 2(1+b)y + b\right] \left[2y - 1 - b\right] \\
& -sy \left[y^2 - (1+b)y + b\right] \left[2pr\lambda_x \left(3x^2 - 2(1+a)x + a\right) - 4\lambda_y y \left(3y - 1 - b\right) \right. \\
& \qquad\qquad\qquad\qquad \left. -ps\lambda_x \left(3y^2 - 2(1+b)y + b\right)\right]
\end{aligned} \tag{3.24}$$

Equation (3.23) and Inequality (3.21) together imply that the singular control u_s is maximizing when

$$G(x, y, \lambda_x, \lambda_y) > 0.$$

■

Notice, if $\psi(t) = 0$ on a non-empty open interval $(t_\alpha, t_\beta) \subset (t_0, t_1)$ and Inequalities 3.15 do *not* hold, then we cannot say whether the singular control u_s is optimal over the interval $[t_\alpha, t_\beta]$.

3.2 Numerical Methods

The optimal control can be numerically calculated under various parameter sets using a forward-backward sweep method [28] using 4^{th} order Runge-Kutta to solve the state equations (3.3) - (3.4) and their corresponding adjoint equations (3.6) - (3.7). This is the same method used to numerically calculate the optimal in the model described in Chapter

2. However, here, we adjust the method to check the Legendre-Clebsch condition (3.15) for any t such that $\psi(t) = 0$. To check this condition numerical, we check if $-\varepsilon < \psi(t) < \varepsilon$, for small ε.

The forward-backward sweep method makes an initial guess for the control u and then solves the state equations (3.3) - (3.4) forward in time using the Runge-Kutta method with the initial conditions (x_0 and y_0). Then, using the state values, the adjoint equations (3.6) - (3.7) are solved backwards in time using the Runge-Kutta method with the transversality conditions (3.8)-(3.9). At this point, the optimal control is updated. For each time t, if $\psi(t) \neq 0$, then $u(t)$ is updated using Equation (3.10). However, if $\psi(t) = 0$, then $u(t)$ is updated using Equation (3.14) provide that inequalities (3.15) hold. The updated control replaces the initial control and the process is repeated until the successive iterates of control values are sufficiently close. The convergence of such an iterative method is based on the work of Hackbush [16]. Other examples using this method can be found in [12, 21, 37].

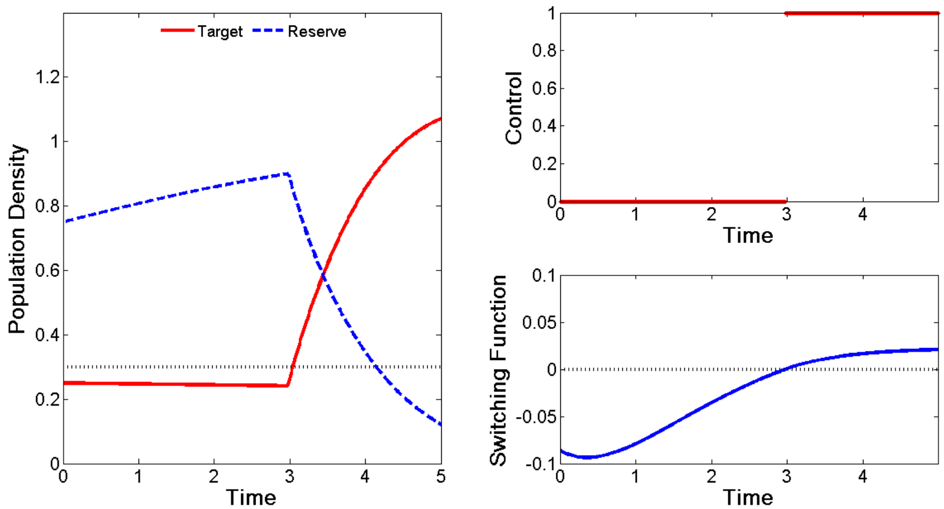
3.3 Numerical Results

In considering various parameter scenarios, the parameter constraints $x_0 < a$ and $y_0 > b$, must be included. For the examples we consider here, we take the minimum threshold for growth for both the target and reserve populations to be 0.3 (that is 30% of each population's carrying capacity), and $x_0 = 0.25$ and $y_0 = 0.75$. Thus, the target population is starting just below its minimum threshold for growth and the reserve population is starting well above its minimum threshold for growth. Additionally, each scenario assumes that the intrinsic growth rate of the reserve population s is greater than the intrinsic growth rate of the target population r, and in each scenario $r = 0.3$.

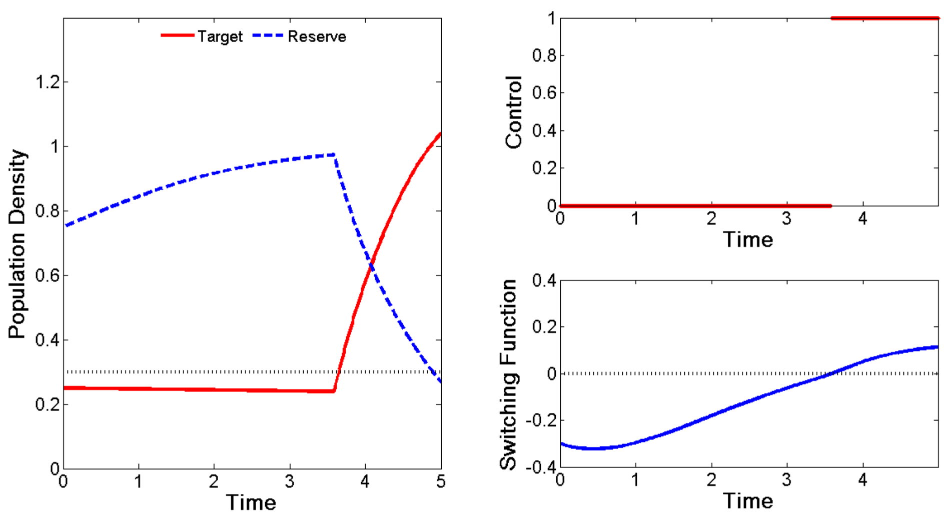
3.3.1 Varying the Intrinsic Growth Rate of the Reserve Population

We first consider the impact of varying the intrinsic growth rate of the reserve population, s. In these scenarios we take $a = 0.3$, $b = 0.3$, $r = 0.3$, $p = 1$, $x_0 = 0.25$, $y_0 = 0.75$, and $A_2 = 0.001$.

In the first scenario we take $s = 0.7$ and $B = 0$ (see Figure 3.1(a)), and in the second scenario we take $s = 1.2$ and $B = 0$ (see Figure 3.1(b)). Since $B = 0$ in each case, no importance is given to maximizing the reserve population at the final time. In each scenario, the qualitative strategy for augmentation is to do nothing for an initial interval of time, then to apply maximum control until the final time. However, when the intrinsic growth rate of the reserve population is lower, the optimal strategy switches from no augmentation to applying maximum augmentation sooner. When $s = 0.7$, the time of the switch is $t = 2.97$, whereas when $s = 1.2$ the time of the switch is $t = 3.58$. When the intrinsic growth rate is lower, the reserve population cannot replenish its population as quickly when being harvested. Thus, in order to maximize the target population, harvesting of the reserve population must start sooner in the case when the reserve intrinsic growth rate is lower.



(a) Lower intrinsic growth rate of $s = 0.7$.



(b) Higher intrinsic growth rate of $s = 1.2$.

Figure 3.1: Scenario for the continuous time optimal control of augmentation in which the parameters are $a = 0.3$, $b = 0.3$, $r = 0.3$, $p = 1$, $x_0 = 0.25$, $y_0 = 0.75$, $A_2 = 0.001$, and $B = 0$. The intrinsic growth rate of the reserve population is $s = 0.7$ in (a) $s = 1.2$ in (b). The graphs on the left show the density of the target (red) and reserve (blue dashed) populations. The black dotted line represents the minimum threshold for growth, $a = b = 0.3$. The top right graphs show the value of the optimal control over time, and the bottom right graphs show the value of the switching function over time. The control switches from no control to applying maximum control at $t = 2.97$ in (a) and $t = 3.58$ in (b).

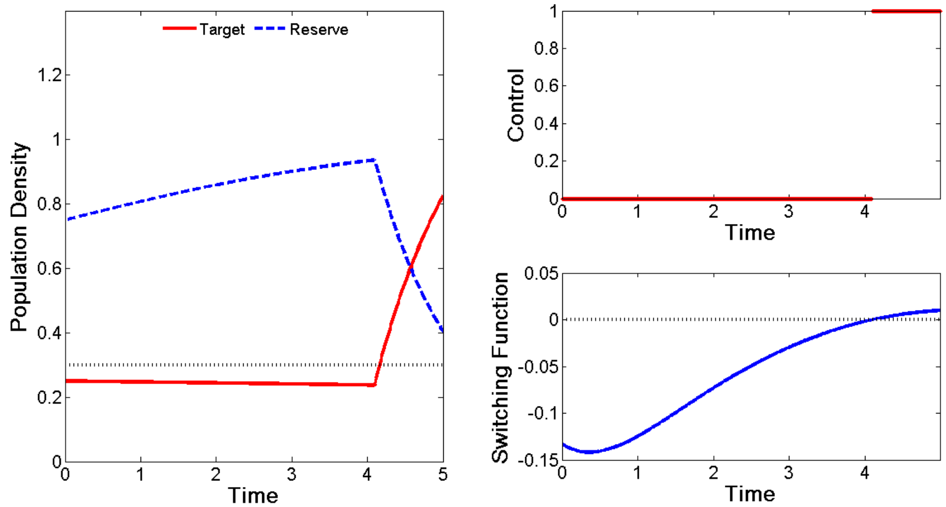
Notice, also that in both scenarios, the reserve population is harvested such that it falls below its minimum threshold for growth, $b = 0.3$ (see black dotted line in Figure 3.1), by the final time. Additionally, in both scenarios, the target population is augmented such that it rises above its carrying capacity at the final time (i.e., $x(t_1) > 1$). We can address the problem of over-harvesting the reserve population by increasing the importance of maximizing the reserve population at the final time, i.e. increasing the value of B.

Thus, in this next set of scenarios we vary the intrinsic growth rate of the reserve population while giving importance to maximizing the reserve population at the final time. In one scenario we take $s = 0.7$ and $B = 0.75$ (see Figure 3.2(a)), and in the other scenario we take $s = 1.2$ and $B = 0.75$ (see Figure 3.2(b)). Since $B = 0.75$ in each case, maximizing the reserve population at the final time is 75% as important as maximizing the target population at the final time.

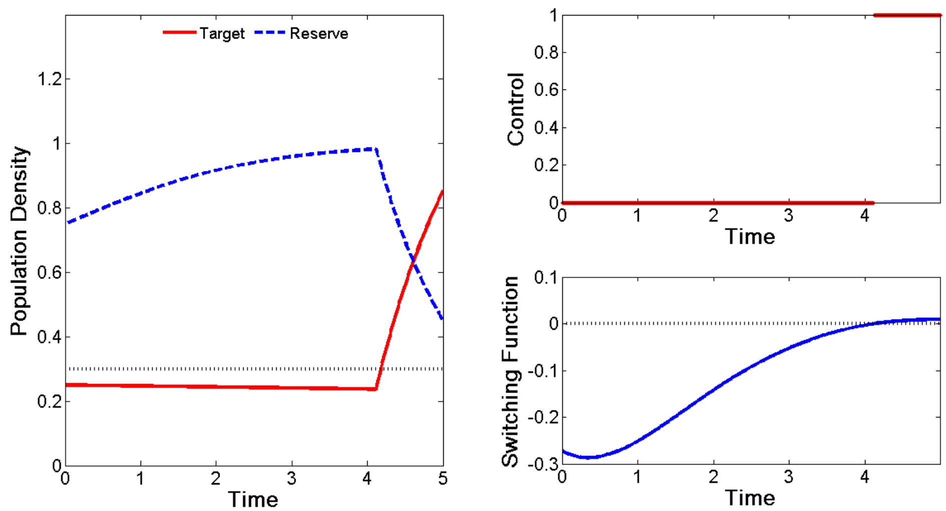
Again, we see the qualitative augmentation strategy in each case is to do nothing for an intial interval of time, then to apply full control until the final time. With these two scenarios, we do not see a great difference in the time at which the optimal strategy switches from no augmentation to maximum augmentation. When $s = 0.7$, the time of the switch is $t = 4.09$, whereas when $s = 1.2$, the time of the switch is 4.11. If the unit of time were one year (i.e. $t = 1$ is one year after the initial time), then the difference between $t = 4.09$ and $t = 4.11$ would be a difference of about 7 days.

Notice that in both scenarios, because of the increased importance of maximizing the reserve populations (as compared to the scenarios in Figure 3.1), the times at which the optimal strategy switches from no augmentation to maximum augmentation are later, and thus less of the reserve population is translocated into the target population. The result on the reserve population is that it stays above its minimum threshold for growth, $b = 0.3$ (see black dotted line in Figure 3.2), at the final time. The result on the target population is that it is not augmented such that it rises above its carrying capacity at the final time (i.e. $x(t_1) < 1$). Indeed this is an ideal scenario for both populations since both the target and reserve populations are between their minimum threshold for growth and their carrying capacities at the final time (i.e. $a < x(t_1) < 1$ and $b < y(t_1) < 1$).

It should be noted that, given the scenarios in Figure 3.2, if B is increased to 1.00, then the optimal augmentation strategy becomes to do no augmentation for the entire time period. When $B = 1.00$, it is just as important to maximize the reserve population at the final time as it is to maximize the target population at the final time. As expected, in this case the reserve population increases over the time period while the target population declines towards extinction.



(a) Lower intrinsic growth rate of $s = 0.7$.



(b) Higher intrinsic growth rate of $s = 1.2$.

Figure 3.2: Scenario for the continuous time optimal control of augmentation in which the parameters are $a = 0.3$, $b = 0.3$, $r = 0.3$, $p = 1$, $x_0 = 0.25$, $y_0 = 0.75$, $A_2 = 0.001$, and $B = 0.75$. The intrinsic growth rate of the reserve population is $s = 0.7$ in (a) $s = 1.2$ in (b). The graphs on the left show the density of the target (red) and reserve (blue dashed) populations. The black dotted line represents the minimum threshold for growth, $a = b = 0.3$. The top right graphs show the value of the optimal control over time, and the bottom right graphs show the value of the switching function over time. The control switches from no control to applying maximum control at $t = 4.09$ in (a) and $t = 4.11$ in (b).

3.3.2 Varying the Ratio of the Reserve Carrying Capacity to the Target Carrying Capacity

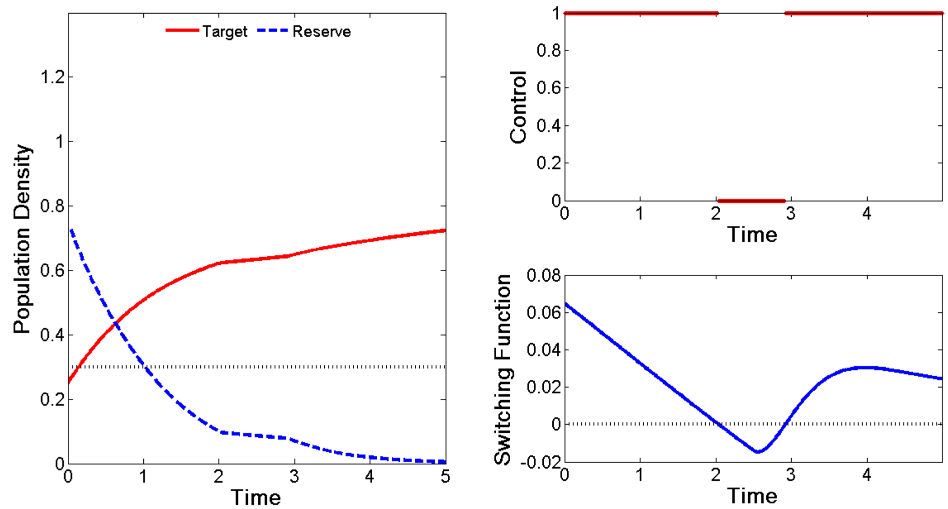
We next consider the effect of varying the ratio of the reserve population carrying capacity to the target population carrying capacity, p. In these scenarios we take $a = 0.3$, $b = 0.3$, $r = 0.3$, $s = 1.2$, $x_0 = 0.25$, $y_0 = 0.75$, and $A_2 = 0.001$.

In the first scenario we take $p = 0.5$ and $B = 0$ (see Figure 3.3(a)), and in the second scenario we take $p = 1.2$ and $B = 0$ (see Figure 3.3(b)). Since $B = 0$ in each case, no importance is given to maximizing the reserve population at the final time. When $p < 1$, the reserve carrying capacity is smaller than the target carrying capacity. Thus, $p = 0.5$ could represent when the reserve population is generated from a captive breeding program or zoo population. When $p > 1$, the reserve carrying capacity is larger than the target carrying capacity. Thus, $p = 1.2$ could represent when the reserve population is a wild, stable (and possibly protected) population.

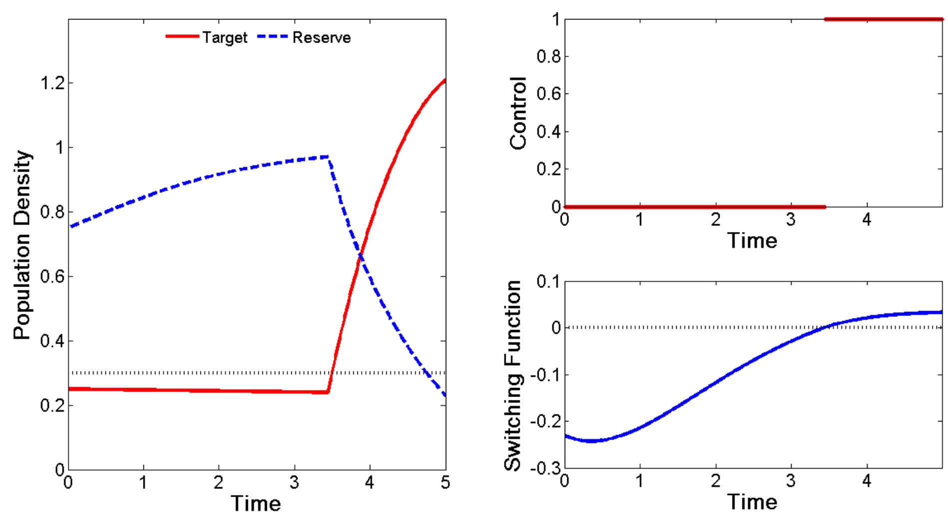
When $p = 1.2$, we see the same qualitative augmentation strategy as in the scenarios shown in Figures 3.1 and 3.2. That is, the optimal augmentation strategy is to do no augmentation for an initial interval of time, then to apply maximum augmentation until the final time. In Figure 3.3(b) the control switches from no control to applying maximum control at $t = 3.44$.

When $p = 0.5$, we see a different qualitative strategy for augmentation emerge. In this case the optimal augmentation strategy is to apply maximum augmentation for some time interval, then do no augmentation for a time interval, then switch back to applying maximum augmentation until the final time. In Figure 3.3(a) the control switches from applying maximum control to no control at $t = 1.81$ and the back to applying maximum control at $t = 2.90$.

Notice in both scenarios, the reserve population is harvested such that it falls below its minimum threshold for growth, $b = 0.3$ (see black dotted line in Figure 3.3), by the final time. In the case of $p = 0.5$, the reserve population is harvested almost to extinction (see Figure 3.3(a)). Additionally, when $p = 1.2$, the target population is augmented such that is rises above its carrying capacity by the final time (i.e. $x(t_1) > 1$). We can address the problem of over-harvesting the reserve population by increasing the importance of maximizing the reserve population at the final time, i.e. increasing the value of B. We utilized this strategy when we looked at scenarios in which we varied the intrinsic growth rate of the reserve population (see Figures 3.1 and 3.2).



(a) Lower ratio of carrying capacities, $p = 0.5$.



(b) Higher ratio of carrying capacities, $p = 1.2$.

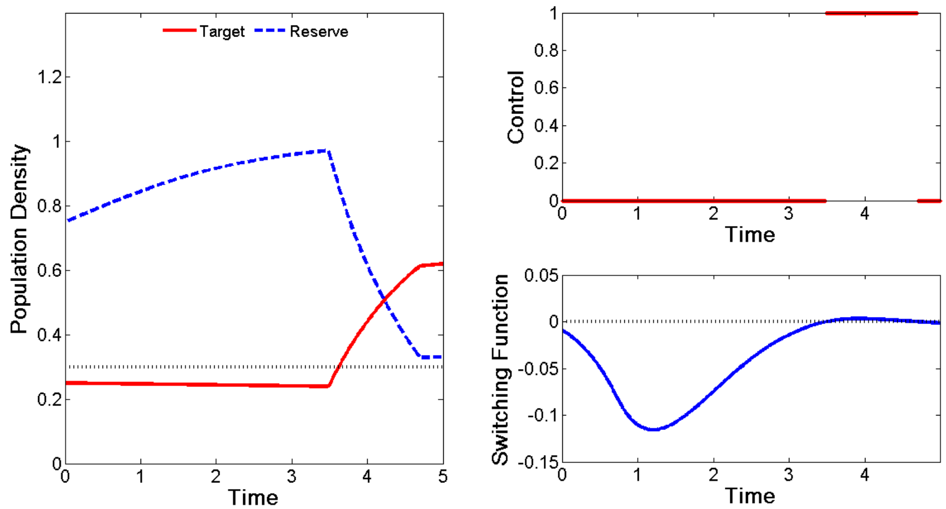
Figure 3.3: Scenario for the continuous time optimal control of augmentation in which the parameters are $a = 0.3$, $b = 0.3$, $r = 0.3$, $s = 1.2$ $x_0 = 0.25$, $y_0 = 0.75$, $A_2 = 0.001$, and $B = 0$. The ratio of the carrying capacities of the reserve population to the target population is $p = 0.5$ in (a) $p = 1.2$ in (b). The graphs on the left show the density of the target (red) and reserve (blue dashed) populations. The black dotted line represents the minimum threshold for growth, $a = b = 0.3$. The top right graphs show the value of the optimal control over time, and the bottom right graphs show the value of the switching function over time. In (a) the control switches from applying maximum control to no control at $t = 1.81$ and the back to applying maximum control at $t = 2.90$. In (b) the control switches from no control to applying maximum control at $t = 3.44$.

Thus, we next consider scenarios similar to those in Figure 3.3 where we increase the importance of maximizing the reserve population at the final time. In one scenario we take $p = 0.5$ and $B = 0.51$ (see Figure 3.4(a)), and in the other scenario we take $p = 1.2$ and $B = 0.45$ (see Figure 3.4(b)). When $B = 0.51$, it is 51% as important to maximize the reserve population at the final time as it is to maximize the target population at the final time. When $B = 0.45$, it is 45% as important to maximize the reserve population at the final time as it is to maximize the target population at the final time. Here the respective B values have been chosen so that reserve population is just above its minimum threshold for growth, $b = 0.3$ (see dotted black line in Figure 3.4), at the final time. In the scenario shown in Figure 3.4(a), we see a reverse of the optimal augmentation strategy in the scenario shown in Figure 3.3(a) where $B = 0$. Here, the qualitative augmentation strategy is for no augmentation to occur for some initial time interval, then for the maximum augmentation to be applied for a time interval, then to switch back to no augmentation. The control switches from no augmentation to maximum augmentation at $t = 3.48$, and then switches back to no augmentation at $t = 4.69$. In the scenario shown in Figure 3.4(b) the optimal augementation strategy is qualitively the same as in the scenario shown in Figure 3.3(b) when $B = 0$. Here, the control switches from no augmentation to maximum augmentation at $t = 3.74$. If the unit of time were one year (i.e. $t = 1$ is one year after the initial time), then the switch to maximum augmentation would occur approximately 3.5 months later in the scenario in Figure 3.4(a) (where $B = 0.45$) than in the scenario in Figure 3.3(b) (where $B = 0$). Notice, in the scenario shown in Figure 3.4(a) the target population is still augmented such that it rises above its carrying capacity by the final time (i.e. $x(t_1) > 1$).

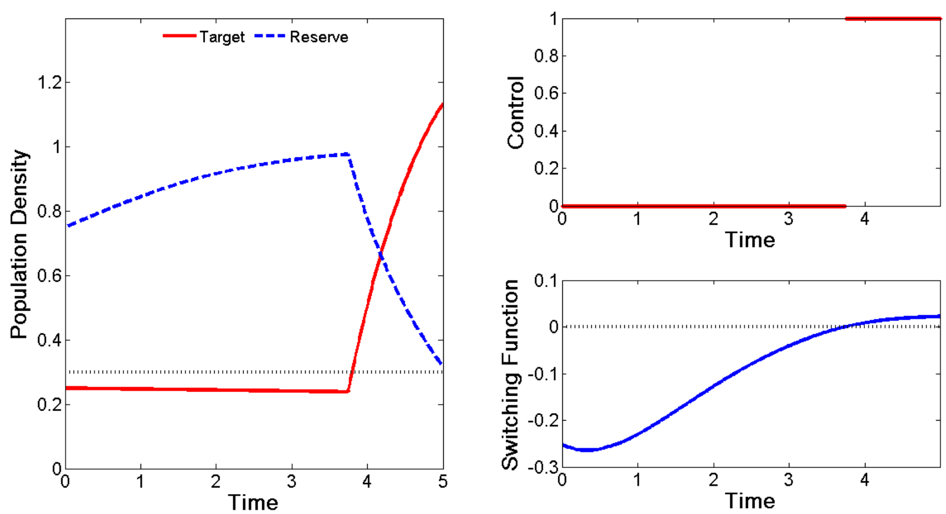
3.4 Conclusions

In this chapter we considered an optimal control formulation for species augmentation which was similar to that explored in Chapter 2, except that here, we assumed the cost associated with translocating individuals from the reserve population to the target population is a linear function of the fraction of the reserve translocated, i.e. we assume the cost coefficients are $A_1 = 0$ and $A_2 > 0$. In determining the characterization of the optimal control for the objective functional in this chapter, we saw that the optimal control on the interior of the control set U is very different from the the optimal control on the interior of the control set for the objective functional used in Chapter 2. Indeed, in this chapter it is possible to have parameter sets for which the singular control u_s (see Equation 3.14) is not optimal over some interval. Using the generalized Legendre-Clebsch Condition, we were able to obtain necessary conditions for u_s being optimal over an interval (see Inequalities 3.15). It should be noted that in the numerical scenarios explored in Section 3.3, the switching function was never identically zero over a nontrivial interval. Thus, we did not encounter a parameter set where the singular control could have occured.

Within the parameter scenarios we did explore, we see a couple of different qualitative augmentation strategies.



(a) Lower ratio of carrying capacities, $p = 0.5$.



(b) Higher ratio of carrying capacities, $p = 1.2$.

Figure 3.4: Scenario for the continuous time optimal control of augmentation in which the parameters are $a = 0.3$, $b = 0.3$, $r = 0.3$, $s = 1.2$ $x_0 = 0.25$, $y_0 = 0.75$, and $A_2 = 0.001$ In (a) $p = 0.5$ and $B = 0.51$, and in (b) $p = 1.2$ and $B = 0.45$. The graphs on the left show the density of the target (red) and reserve (blue dashed) populations. The black dotted line represents the minimum threshold for growth, $a = b = 0.3$. The top right graphs show the value of the optimal control over time, and the bottom right graphs show the value of the switching function over time. In (a) the control switches from no augmentation to maximum augmentation at $t = 3.48$, and then switches back to no augmentation at $t = 4.69$. In (b) the optimal control switches from no augmentation to applying maximum augmentation at $t = 3.74$.

(1) No augmentation over an initial time interval, then apply maximum augmentation effort until the final time.

(2) Apply maximum augmentation effort over an initial time interval, then have no augmentation over another time interval, then switch back to applying maximum augmentation effort until the final time.

(3) No augmentation for an initial time interval, then apply maximum augmentation effort for some time interval, then switch back to no augmentation for the remainder of the time horizon.

(4) No augmentation over the entire time horizon.

Of the different parameter scenarios explored in this chapter, qualitative augmentation strategy (1) was optimal most often. However, the time at which the switch occurs (from no augmentation to applying maximum augmentation effort) varies based on the parameter set. Qualitative augmentation strategy (2) was only optimal in one of the parameter scenarios considered. This scenario had a low ratio of reserve population carrying capacity to target population carrying capacity ($p = 0.5$), and no importance was given to maximizing the reserve population at the final time ($B = 0$). In the scenario in Figure 3.3(a), when the importance of maximizing the reserve population at the final time was increased to $B = 0.51$ (see Figure 3.4(a)) we encountered the only one of the parameter scenarios explored where qualitative augmentation strategy (3) was optimal. Lastly, we only found qualitative augmentation strategy (4) to be optimal when the importance of maximizing the reserve population at the final time equaled the importance of maximizing the target population at the final time, i.e. $B = 1$ (like scenarios from Figure 3.2, but with $B = 1$).

In the scenarios where we varied the intrinsic growth rate of the reserve population we saw that qualitative augmentation strategy (1) was optimal for each scenario. However, from the scenarios shown (Figures 3.1 and 3.2) we observed that a larger intrinsic growth rate led to the time of the switch from no augmentation to applying maximum augmentation effort occurring later, though the difference in times may be small. Additionally, we observed that increasing the importance of maximizing the reserve population at the final time (i.e. increasing B, compare Figure 3.1 to Figure 3.2) also leads to the time of the switch from no augmentation to applying maximum augmentation effort occuring later. Lastly, we observed that increasing the importance of maximizing the reserve population too high could lead to the optimal augmentation strategy being no augmentation occurring at all.

In the scenarios where we varied the ratio of the reserve carrying capacity to the target carrying capacity, we saw a variety of different qualitative optimal augmentation strategies (specifically strategies (1), (2), and (3)). In each set of scenarios (see Figures 3.3 and 3.4) we observed that given the same parameters for all else, having $p < 1$ and $p > 1$ led to different qualitative optimal augmentation strategies (at least in the scenarios we considered). When no importance was given to maximizing the reserve population at the final time ($B = 0$), the optimal augmentation strategy would cause the reserve population to inevitably decline to extinction for both $p = 0.5$ and $p = 1.2$ (see Figure 3.3). However, in the scenario in Figure 3.4 we found the minimum value of B in each case ($p = 0.5$ and $p = 1.2$) such that the reserve population remained above its minimum threshold for growth.

What is most important to conclude from the different parameter scenarios is that these numerical simulations can tell natural resource managers the best they can do given a certain scenario, and what augmentation strategy will yield that "best" outcome. In comparing different parameter scenarios, there were some optimal augmentation strategies that differed only by a few days in determining when to start applying maximum augmentation effort. In comparing other scenarios, we found completely different qualitative optimal augmentation strategies. It is important for natural resource managers to be able to explore what parameter scenarios lead to these drastically different augmentation strategies.

Chapter 4

Discrete Time Model (Augment then Grow)

Having considered continuous time models of augmentation, why do we now choose to analyze a discrete version? First, when augmentations have been carried out in the field, the actual translocation/augmentation event occurs at one or a few discrete times. In the case of the Florida panther , one augmentation event occurred in 1995 when eight female Texas panthers where translocated into the Florida panther range [14, 27]. In the case of the Cabinet Mountain grizzly bears, four discrete augmentation events, in which one individuals was moved each time, occurred over a three year period [38]. Thus, it is appropriate to consider models and optimal control frameworks which allow for discrete augmentation events.

Secondly, many of the populations which have been augmented and are under consideration for augmentation, have a distinct seasonal birth pulse. For example, the grizzly bear (*Ursus arctos horribilis*) breeding season is between mid-May to July. Cubs conceived during a breeding season are born the following year from January to March [30]. Given these types of natural population dynamics, it would be appropriate to model a population under consideration for augmentation in discrete time with a time step of one year.

4.1 A Discrete Model for Species Augmentation

Consider two populations of the same species: N, a target/endangered population, and R, a reserve population. We assume that, at the initial time, the endangered population is declining due to small population size. For the reserve population to be a viable source for harvesting individuals with which to augment the target population, it must be at equilibrium or growing at the initial time. Thus, in the absence of augmentation the target and reserve populations grow according to logistic-type discrete difference equations

$$N_{k+1} - N_k = rN_k \left(\frac{N_k}{K_N} - a \right) \left(1 - \frac{N_k}{K_N} \right), \tag{4.1}$$

$$R_{k+1} - R_k = sR_k \left(\frac{R_k}{K_R} - b \right) \left(1 - \frac{R_k}{K_R} \right) \tag{4.2}$$

respectively, where N_k and R_k are the target and reserve population sizes at time step k, r and s are the intrinsic growth rates of N and R, respectively, and K_N and K_R are the carrying capacities of N and R, respectively. The model is constructed so for $N_k < aK_N$ and $R_k < bK_R$, the endangered and reserve populations, respectively, are declining. This density dependent population decline is known as the Allee Effect.

4.1.1 Selecting the Order of Events

In using discrete models, the order in which events take place is very important. For the underlying model described in Equations (4.1) and (4.2), there are two possibilities:

(I) at each time step we can harvest and augment, and then let the populations grow, or

(II) let the populations grow, and then harvest and augment.

In some augmentation projects it might be best to augment prior to the breeding season, but in other cases wildlife managers may be limited to augmenting when individuals become available. Thus, we will consider both cases. Case I is addressed in this chapter, and case II in the next chapter. We investigate how the change in order will affect the optimal augmentation strategy.

In each case, we assume the object of augmentation is to maximize the target population and the reserve population (weighted by some factor to be less important) at a given final time T while minimizing the cost of translocating individuals. We assume that the total population $(N + R)$ is to be maximized by the final time, with different relative weights applied to the reserve and target populations. We assume it is not as important to maximize the reserve population as the target population by the final time. In each case, we have a vector of controls $u = (u_0, \dots, u_{T-1})$ where u_k is the control applied at time step k, the fraction of the reserve population that is harvested and translocated to the target population.

4.1.2 A Model for the Augment then Grow Case

If we harvest and augment first and then let the populations grow the system in Equations (4.1)-(4.2) becomes

$$N_{k+1} = (N_k + u_k R_k) \left[r \left(\frac{N_k + u_k R_k}{K_N} - a \right) \left(1 - \frac{N_k + u_k R_k}{K_N} \right) + 1 \right], \tag{4.3}$$

$$R_{k+1} = (R_k - u_k R_k) \left[s \left(\frac{R_k - u_k R_k}{K_R} - b \right) \left(1 - \frac{R_k - u_k R_k}{K_R} \right) + 1 \right]. \tag{4.4}$$

Rescaling these two populations with respect to their carrying capacities ($x_k \equiv \frac{N_k}{K_N}$ and $y_k \equiv \frac{R_k}{K_R}$) gives

$$x_{k+1} = (x_k + pu_k y_k)\left[r\left(x_k + pu_k y_k - a\right)\left(1 - x_k - pu_k y_k\right) + 1\right], \quad (4.5)$$

$$y_{k+1} = (y_k - u_k y_k)\left[s\left(y_k - u_k y_k - b\right)\left(1 - y_k + u_k y_k\right) + 1\right]. \quad (4.6)$$

where $p \equiv K_R/K_N$, i.e. the ratio of the reserve carrying capacity to the endangered carrying capacity. Thus, we have a vector for each state, $x = (x_0, \ldots, x_T)$ and $y = (y_0, \ldots, y_T)$, where x_k and y_k are the densities of the target and reserve populations, respectively at time step k, and the initial densities, x_0 and y_0 are known. Notice that since we are modeling population densities, we ignore issues that arise in discrete modeling with counting fractional individuals. As usual in discrete optimal control problems, the state vectors have one more component than the control vectors. We assume that the target population x has an initial density x_0 below its minimum threshold for growth a, and that the reserve population y has an initial density y_0 above its minimum threshold for growth b, i.e. $x_0 < a$ and $y_0 > b$. Thus, the optimal control formulation is

$$\max_{u \in U}\left[x_T + By_T - \sum_{n=0}^{T-1}\left(A_1 u_n^2 + A_2 u_n\right)\right] \quad (4.7)$$

where

$$U = \{u = (u_0, \ldots, u_{T-1}) \mid 0 \leq u_k \leq 0.9,\ k = 0, 1, \ldots, T-1\} \quad (4.8)$$

and for $k = 0, 1, \ldots, T-1$

$$x_{k+1} = (x_k + pu_k y_k)\left[r\left(x_k + pu_k y_k - a\right)\left(1 - x_k - pu_k y_k\right) + 1\right], \quad (4.9)$$

$$x_0 < a \quad (4.10)$$

$$y_{k+1} = (y_k - u_k y_k)\left[s\left(y_k - u_k y_k - b\right)\left(1 - y_k + u_k y_k\right) + 1\right], \quad (4.11)$$

$$y_0 > b. \quad (4.12)$$

In the previous two chapters were the target and reserve populations were modeled with differential equations (the continuous case), we allowed the control variable to vary between 0 and 1. In the continuous case, the control variable represented a rate of movement from the reserve population to the target population. However, in this discrete case, the control variable, u represents the proportion of the reserve population moved at each time step. In order to prevent moving the entire reserve population into the target population at a particular time step, we only allow the control u to vary between 0 and 0.9. That is to say no more than 90% of the reserve population can be translocated to the target population at any particular time step.

We refer to the function being maximized as the objective functional, denoted

$$J(u) = x_T + By_T - \sum_{n=0}^{T-1} \left(A_1 u_n^2 + A_2 u_n \right). \tag{4.13}$$

Using this objective functional, we are maximizing the target population at the final time, maximizing the reserve population at the final time (but weighted by the constant $0 < B < 1$), and minimizing the cost associated with translocated individuals from the reserve population to the target population over the time steps $(0, 1, \ldots, T-1)$. The cost term, $A_1 u_k^2$, which has quadratic dependence on u_k, accounts for nonlinear increases in the costs of translocation as the fraction translocated at a given time step increases. The cost term $A_2 u_k$, which has linear dependence on u_k, accounts for linear increases in the costs of translocation as the fraction translocated at a given time step increases. Note that we assume $A_1 \geq 0$ and $A_2 \geq 0$.

4.2 Concavity of the Hamiltonian

In order to utilize Pontryagin's Maximum Principle, the Hamiltonian, H_k, must satisfy the concavity condition

$$\frac{\partial^2 H_k}{\partial u_k^2} \leq 0 \tag{4.14}$$

for all time steps k [7].

Were we to use Pontryagin's Maximum Principle to determine a characterization for the optimal control we would have to construct the Hamiltonian function

$$\begin{aligned} H_k \quad = \quad & -A_1 u_k^2 - A_2 u_k + \lambda_{x,k+1}(x_k + pu_k y_k) \left[r(x_k + pu_k y_k - a)(1 - x_k - pu_k y_k) + 1 \right] \\ & + \lambda_{y,k+1}(1 - u_k) y_k \left[s\left((1-u_k) y_k - b \right) \left(1 - (1-u_k) y_k \right) + 1 \right], \end{aligned} \tag{4.15}$$

where $\lambda_{x,k+1}$ and $\lambda_{y,k+1}$ are adjoint variables corresponding to the state variables x_k and y_k, respectively. Expanding the products after $\lambda_{x,k+1}$ in Equation (4.15) we obtain

$$
\begin{aligned}
&(x_k + pu_k y_k)\left[r(x_k + pu_k y_k - a)(1 - x_k - pu_k y_k) + 1\right] \\
&\quad = (x_k + pu_k y_k)\left[r\left(x_k - x_k^2 - 2px_k u_k y_k + pu_k y_k - p^2 u_k^2 y_k^2 - a + ax_k + apu_k y_k\right) + 1\right] \\
&\quad = (x_k + pu_k y_k)\left[-rx_k^2 + r(1+a)x_k - ar + \left[r(1+a) - 2rx_k\right] pu_k y_k - rp^2 u_k^2 y_k^2 + 1\right] \\
&\quad = -rx_k^3 + r(1+a)x_k^2 - arx_k + \left[r(1+a)x_k - 2rx_k^2\right] pu_k u_k - rp^2 x_k u_k^2 y_k^2 + x_k \\
&\qquad - rpx_k^2 u_k y_k + rp(1+a)x_k u_k y_k - arpu_k y_k + \left[r(1+a) - 2rx_k\right] p^2 u_k^2 y_k^2 \\
&\qquad - rp^3 u_k^3 y_k^3 + pu_k y_k \\
&\quad = -rx_k^3 + r(1+a)x_k^2 + (1 - ra)x_k + \left[-3rx_k^2 + 2r(1+a)x_k + (1 - ra)\right] pu_k y_k \\
&\qquad - \left[3rx_k - r(1+a)\right] p^2 u_k^2 y_k^2 - rp^3 u_k^3 y_k^3.
\end{aligned}
$$

Expanding the product after $\lambda_{y,k+1}$ in Equation (4.15) we get

$$
\begin{aligned}
&(y_k - u_k y_k)\left[s\left(y_k - u_k y_k - b\right)\left(1 - y_k + u_k y_k\right) + 1\right] \\
&\quad = (y_k - u_k y_k)\left[s\left(y_k - y_k^2 + 2u_k y_k^2 - u_k y_k - u_k^2 y_k^2 - b + by_k - bu_k y_k\right) + 1\right] \\
&\quad = (y_k - u_k y_k)\left[-sy_k^2 + s(1+b)y_k - sb + 2su_k y_k^2 - s(1+b)u_k y_k - su_k^2 y_k^2 + 1\right] \\
&\quad = -sy_k^3 + s(1+b)y_k^2 - sby_k + 2su_k y_k^3 - s(1+b)u_k y_k^2 - su_k^2 y_k^3 + y_k \\
&\qquad + su_k y_k^3 - s(1+b)u_k y_k^2 + sbu_k y_k - 2su_k^2 y_k^3 + s(1+b)u_k^2 y_k^2 + su_k^3 y_k^3 - u_k y_k \\
&\quad = -sy_k^3 + s(1+b)y_k^2 + (1 - sb)y_k + \left[3sy_k^3 - 2s(1+b)y_k^2 - (1 - sb)y_k\right] u_k \\
&\qquad - \left[3sy_k^3 - s(1+b)y_k^2\right] u_k^2 + su_k^3 y_k^3.
\end{aligned}
$$

Thus, we can write the Hamiltonian as

$$
\begin{aligned}
H_k \quad = \quad & -A_1 u_k^2 - A_2 u_k \\
& + \lambda_{x,k+1}\left\{-rx_k^3 + r(1+a)x_k^2 + (1 - ra)x_k + \left[-3rx_k^2 + 2r(1+a)x_k + (1 - ra)\right] pu_k y_k \right. \\
& \qquad \left. - \left[3rx_k - r(1+a)\right] p^2 u_k^2 y_k^2 - rp^3 u_k^3 y_k^3\right\} \\
& + \lambda_{y,k+1}\left\{-sy_k^3 + s(1+b)y_k^2 + (1 - sb)y_k + \left[3sy_k^3 - 2s(1+b)y_k^2 - (1 - sb)y_k\right] u_k \right. \\
& \qquad \left. - \left[3sy_k^3 - s(1+b)y_k^2\right] u_k^2 + su_k^3 y_k^3\right\}
\end{aligned} \tag{4.16}
$$

Now, let

$$
\begin{aligned}
f_{A,k}(x_k, y_k, \lambda_{x,k+1}, \lambda_{y,k+1}) &= -rp^3\lambda_{x,k+1}y_k^3 + s\lambda_{y,k+1}y_k^3 \\
f_{B,k}(x_k, y_k, \lambda_{x,k+1}, \lambda_{y,k+1}) &= A_1 + \lambda_{x,k+1}\left[3rx_k - r(1+a)\right]p^2y_k^2 \\
&\quad + \lambda_{y,k+1}\left[3sy_k - s(1+b)\right]y_k^2 \\
f_{C,k}(x_k, y_k, \lambda_{x,k+1}, \lambda_{y,k+1}) &= -A_2 + \lambda_{x,k+1}\left[-3rx_k^2 + 2r(1+a)x_k + (1-ra)\right]py_k \\
&\quad + \lambda_{y,k+1}\left[3sy_k^2 - 2s(1+b)y_k - (1-sb)\right]y_k \\
f_{D,k}(x_k, y_k, \lambda_{x,k+1}, \lambda_{y,k+1}) &= \lambda_{x,k+1}\left[-rx_k^3 + r(1+a)x_k^2 + (1-ra)x_k\right] \\
&\quad + \lambda_{y,k+1}\left[-sy_k^3 + s(1+b)y_k^2 + (1-sb)y_k\right].
\end{aligned}
$$

Thus, we can rewrite the Hamiltonian as

$$H_k = f_{A,k}u_k^3 - f_{B,k}u_k^2 + f_{C,k}u_k + f_{D,k} \tag{4.17}$$

The second derivative of the Hamiltonian at time step k with respect to the control at time step k using the form of the Hamiltonian given in Equation (4.17) is

$$\frac{\partial^2 H_k}{\partial u_k^2} = 6f_{A,k}u_k - 2f_{B,k}. \tag{4.18}$$

Since we cannot guarantee that

$$\frac{\partial^2 H_k}{\partial u_k^2} \leq 0$$

for all parameter sets, we cannot utilize Pontryagin's Maximum Principle for this particular control problem. See [7] for an example in which the optimal control does not maximize the Hamiltonian with respect to the controls due the lack of concavity. Thus, we turn to numerical methods to solve our optimal control problem.

4.3 Numerical Methods

Due to the fact that we cannot utilize Pontryagin's Maximum Principle, we must resort to a numerical method that directly maximizes the objective functional,

$$J(u) = x_T + By_T - \sum_{n=0}^{T-1}\left(A_1u_n^2 + A_2u_n\right).$$

We discretize the range of the control and search for the control that maximizes J. To accomplish this, we first define how fine the control space U will be discretized. Recall, each u_k must be in the interval $[0, 0.9]$, for $k = 0, \ldots, T-1$. Let n be the number of discrete values of u_k in the interval $[0, 0.9]$, and let

$$h = \frac{0.9 - 0}{n - 1} = \frac{0.9}{n - 1}.$$

Thus, given an n, the possible discrete values for u_k are given in the set

$$U_{mesh} = \{0, h, 2h, 3h, \cdots, (n-2)h, 0.9\}.$$

Next, evaluate the objective functional for all possible permutations of the components of u. If for example, $T = 5$ and $n = 10$, then

$$u = (u_0, u_1, u_2, u_3, u_4),$$

and there are $5^{10} = 9,765,625$ possible permutations for u. Note, the objective functional depends not only on u, but also on x_T and y_T. Thus, given a permutation of u, we first solve for x_T and y_T using Equations (4.9) and (4.11), respectively. Then, using x_T, y_T, and u, we evaluate $J(u)$. In evaluating the objective functional for each u, we can determine which u maximizes the objective functional. For this numerical method, the vector u that maximizes the objective functional will be referred to as the optimal control. For a problem with more time steps or a much finer mesh for U_{mesh}, a more efficient numerical algorithm will be needed.

4.4 Numerical Results

In considering various parameter scenarios, the parameter constraints on x_0 and y_0, $x_0 < a$ and $y_0 > b$, must be included. For the examples included here, we take the minimum threshold for growth for both the target and reserve populations to be 0.3 (that is 30% of each populations' carrying capacity), and $x_0 = 0.25$ and $y_0 = 0.70$. Thus, the target population is starting just below its minimum threshold for growth, and the reserve population is starting well above its minimum threshold for growth. For each of the following scenarios, we use parameters $a = 0.30$, $b = 0.30$, $r = 0.30$, $x_0 = 0.25$, and $y_0 = 0.70$, and vary the values of s, p, A_1, A_2 and B. Additionally, in each of the scenarios, assume $T = 5$ unless otherwise states. Lastly, in each of the following scenarios we let $n = 18$ which corresponds to $h = 0.05$, and thus

$$U_{mesh} = \{0, 0.05, 0.10, \ldots, 0.85, 0.90\}.$$

Here, we are looking for qualitative results, and thus requiring a finer mesh for U_{mesh} is unneccessary. Furthermore, since we are considering small population sizes, it is reasonable to consider 5% increments in u_k. Thus, for this application, the level of accuracy of each u_k is appropriate.

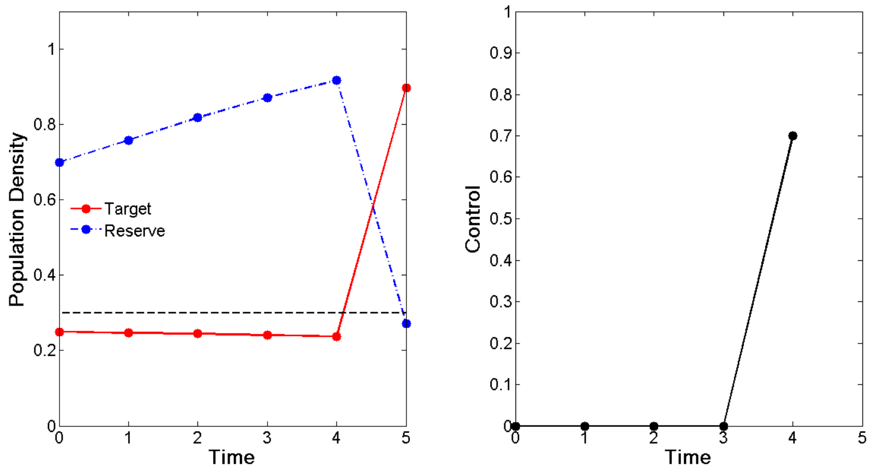


Figure 4.1: Simulation for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.30$, $s = 0.70$, $p = 1.00$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 0.10$, $A_2 = 0.70$, $B = 0.00$, with $h = 0.05$. The left graph shows the density of the target (red) and reserve (blue dashed) populations at each time step. The right graph shows the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control in this simulation are $u = [0.00\ 0.00\ 0.00\ 0.00\ 0.80]$.

4.4.1 Varying the Linear Cost of Translocation

The first scenario we consider takes $s = 0.7$, $p = 1$, $A_1 = 0.10$, $A_2 = 0.70$ and $B = 0$. Thus, no importance is given to maximizing the reserve population at the final time. The results for this scenario are shown in Figure 4.1. Note the values for the optimal control in this simulation are

$$u = [0.00\ 0.00\ 0.00\ 0.00\ 0.80],$$

and thus the only augmentation occurs at time step $k = 4$ when 80% of the reserve population is translocated to the target population. In this simulation we see that though the target population is augmented to be above its minimum threshold for growth ($a = 0.30$) at the final time, the proportion of the reserve population moved is so large that the reserve population falls below its minimum threshold for growth ($b = 0.30$) at the final time. However, recall in this simulation $B = 0$ and thus no importance is placed on maximizing the reserve population at the final time.

If we increase the importance of maximizing the reserve population at the final time, we would expect a smaller proportion of the reserve population to be translocated into the target population. This is indeed what we find in the next simulation where $s = 0.7$, $p = 1$, $A_1 = 0.10$, $A_2 = 0.70$ and $B = 0.25$. Thus, in this scenario, it is 25% as important to maximize the reserve population as it is to maximize the target population. The results for this scenario are shown in Figure 4.2. Note the values for the optimal control in this simulation are

$$u = [0.00\ 0.00\ 0.30\ 0.00\ 0.00],$$

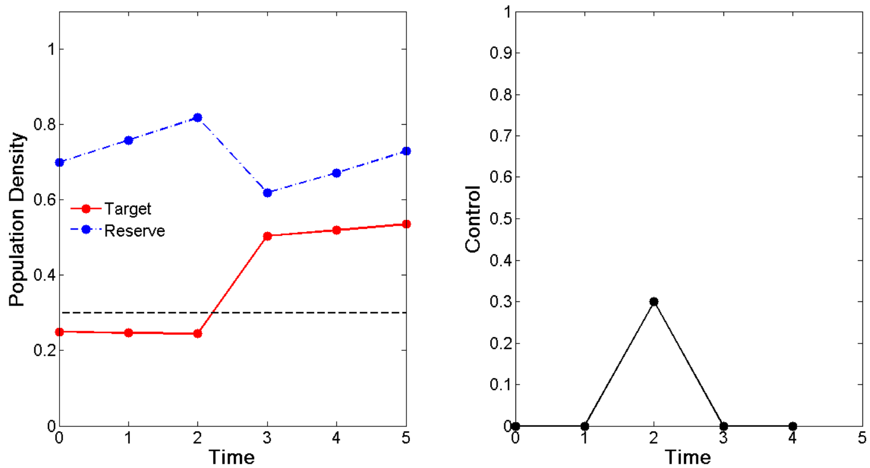


Figure 4.2: Simulation for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.30$, $s = 0.70$, $p = 1.00$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 0.10$, $A_2 = 0.70$, $B = 0.25$, with $h = 0.05$. The left graph shows the density of the target (red) and reserve (blue dashed) populations at each time step. The right graph shows the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control in this scenario are $u = [0.00\ 0.00\ 0.30\ 0.00\ 0.00]$.

and thus the only augmentation occurs at time step $k = 2$ when 30% of the reserve population is translocated to the target population. In this simulation we see that the augmentation at time step $k = 2$ leads to both the target and reserve populations being above their minimum thresholds for growth ($a = b = 0.30$) at the final time. Notice also that increasing the importance of maximizing the reserve population at the final time led to a optimal control where the augmentation occurs earlier in the time horizon and where a smaller proportion of the reserve population is translocated.

In the next three scenarios, we consider the effects of lowering and raising the cost of translocation by adjusting the values of A_2. We first consider lowering the cost of translocation by lowering A_2 from 0.70 to 0.50. Thus, in this next scenario $s = 0.7$, $p = 1$, $A_1 = 0.10$, $A_2 = 0.50$, and $B = 0.25$. The results for this scenario are shown in Figure 4.3. Note the values for the optimal control in this simulation are

$$u = [0.00\ 0.00\ 0.00\ 0.50\ 0.00],$$

and thus the only augmentation occurs at time step $k = 3$ when 50% of the reserve population is translocated to the target population. As in the previous simulation (see Figure 4.2), we see that the augmentation leads to both the target and reserve populations being above their minimum thresholds for growth ($a = b = 0.30$) at the final time. However, in this simulation where the cost is lower, the augmentation occurs later (time step $k = 3$ instead of $k = 2$) and the optimal augmentation strategy requires a larger proportion of the

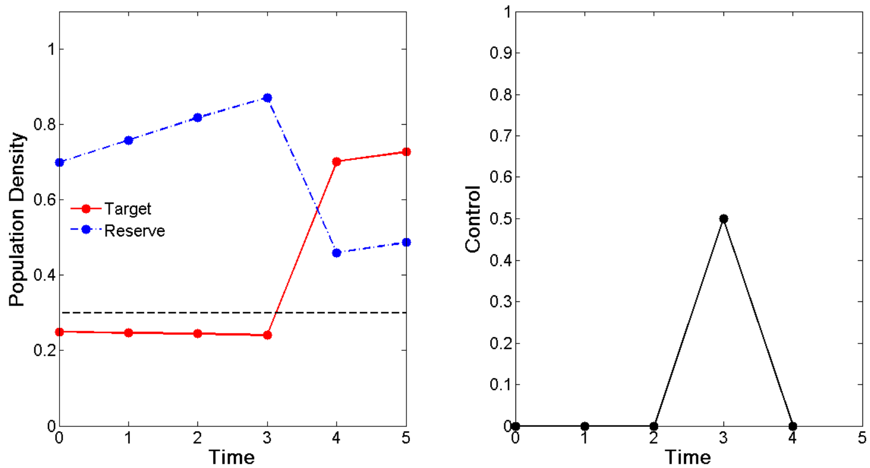


Figure 4.3: Simulation for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.30$, $s = 0.70$, $p = 1.00$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 0.10$, $A_2 = 0.50$, $B = 0.25$, with $h = 0.05$. The left graph shows the density of the target (red) and reserve (blue dashed) populations at each time step. The right graph shows the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control in this simulation are $u = [0.00\ 0.00\ 0.00\ 0.50\ 0.00]$.

reserve population be translocated (50% as opposed to 30% in the scenario shown in Figure 4.2).

In the next scenario, we consider a higher cost of translocation by raising A_2 from 0.70 to 0.80, thus we let $s = 0.7$, $p = 1$, $A_1 = 0.10$, $A_2 = 0.80$, and $B = 0.25$. The results for this scenario are shown in Figure 4.4. Note the values for the optimal control in this simulation are

$$u = [0.00\ 0.00\ 0.15\ 0.00\ 0.00],$$

and thus the only augmentation occurs at time step $k = 2$ when 15% of the reserve population is translocated to the target population. Notice, in this simulation, though the time step at which the augmentation occurs ($k = 2$) remains the same as when $A_2 = 0.70$ (see Figure 4.2), the proportion of the reserve population that is translocated is reduced from 30% to 15%. Notice in Figures 4.2, 4.3, and 4.4 both the target and reserve populations are above their minimum thresholds for growth and below their carrying capacities at the final time. The reserve being harvested such that it does not fall below its minimum threshold for growth is due to the fact that some importance is given to the maximizing the reserve population at the final time ($B = 0.25$ in these three scenarios).

If the linear cost coefficient is increased further by raising A_2 from 0.80 to 0.90 (letting $s = 0.7$, $p = 1$, $A_1 = 0.10$, $A_2 = 0.90$, and $B = 0.25$), we find that the optimal augmentation strategy is to not augment at all. The results for this scenario are shown in Figure 4.5. Note that the values for the optimal control in this scenario are

$$u = [0.00\ 0.00\ 0.00\ 0.00\ 0.00],$$

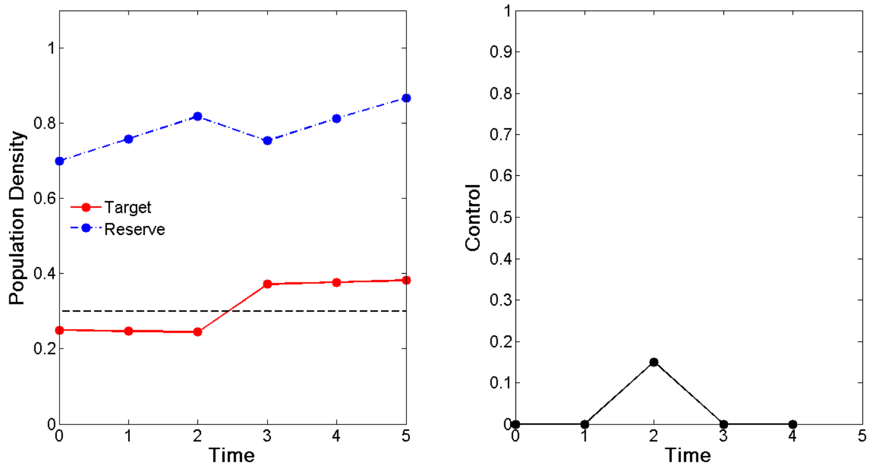


Figure 4.4: Simulation for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.30$, $s = 0.70$, $p = 1.00$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 0.10$, $A_2 = 0.80$, $B = 0.25$, with $h = 0.05$. The left graph shows the density of the target (red) and reserve (blue dashed) populations at each time step. The right graph shows the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control in this simulation are $u = [0.00\ 0.00\ 0.15\ 0.00\ 0.00]$.

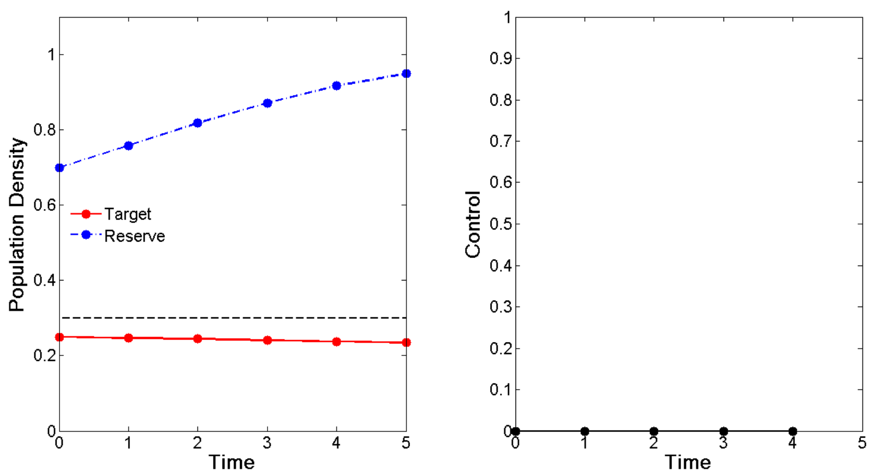


Figure 4.5: Simulbtion for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.30$, $s = 0.70$, $p = 1.00$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 0.10$, $A_2 = 0.90$, $B = 0.25$, with $h = 0.05$. The left graph shows the density of the target (red) and reserve (blue dashed) populations at each time step. The right graph shows the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control in this simulation are $u = [0.00\ 0.00\ 0.00\ 0.00\ 0.00]$.

and thus the optimal augmentation strategy is to do nothing. In this case, the cost of translocation is so high that it prohibits moving any individuals from the reserve population to the target population.

4.4.2 Assuming Only a Linear Cost of Translocation

In the objective functional there are two cost terms

$$\sum_{k=0}^{T-1} A_1 u_k^2 \quad \text{and} \quad \sum_{k=0}^{T-1} A_2 u_k.$$

Recall, the first term captures costs that increase quadratically as an increased proportion of the reserve population is translocated to the target population, while the second term captures costs that increase linearly. In this next scenario, we examine what occurs when the cost is lowered by removing the costs that increase quadratically, i.e. by letting $A_1 = 0$, $A_2 = 0.70$, and $B = 0.25$. Note that though taking $A_1 = 0$ makes the objective functional linear with respect to the control, the underlying state equations retain their nonlinearity with respect to the control. Since $B = 0.25$, it is 25% as important to maximize the reserve population at the final time as it is to maximize the target population at the final time. The results for this scenario are shown in Figure 4.6. Note that the values for the optimal control in this simulation are

$$u = [0.00\ 0.00\ 0.35\ 0.00\ 0.00],$$

and thus the only augmentation occurs at time step $k = 2$ when 35% of the reserve population is translocated to the target population. Notice, in this simulation, though the time step at which the augmentation occurs ($k = 2$) remains the same as when $A = 0.10$ and $A_2 = 0.70$ (see Figure 4.2), the proportion of the reserve population that is translocated is increase from 30% to 35%. Thus, we see when the cost is lowered, the proportion of the reserve population that it is optimal to translocate is increased.

4.4.3 Varying the Time Horizon

In the next two scenarios, we consider what happens when the time horizon is extended or shortened, i.e. when T is larger or smaller than 5. We first examine what occurs when the time horizon is extended. In this scenario we let $s = 0.7$, $p = 1$, $A_1 = 0.10$, $A_2 = 0.70$, $B = 0.25$, and $T = 6$. The results for this scenario are shown in Figure 4.7. Note the value for the optimal control in this scenario is

$$u = [0.00\ 0.00\ 0.35\ 0.00\ 0.00\ 0.00],$$

and thus the only augmentation occurs at time step $k = 2$ when 35% of the reserve population is translocated to the target population. Comparing to the similar scenario where $A_1 = 0.10$, $A_2 = 0.70$, $B = 0.25$, and $T = 5$ (see Figure 4.2), we see the same

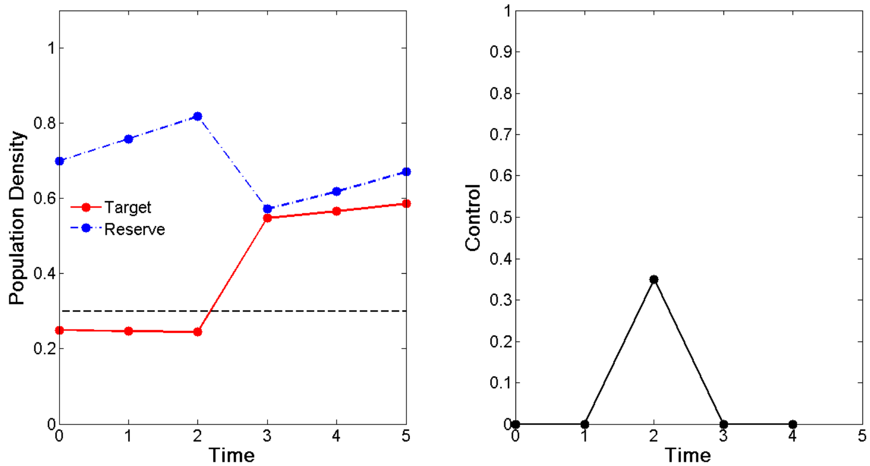


Figure 4.6: Simulation for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.30$, $s = 0.70$, $p = 1.00$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 0.00$, $A_2 = 0.70$, $B = 0.25$, with $h = 0.05$. The left graph shows the density of the target (red) and reserve (blue dashed) populations at each time step. The right graph shows the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control in this simulation are $u = [0.00\ 0.00\ 0.35\ 0.00\ 0.00]$.

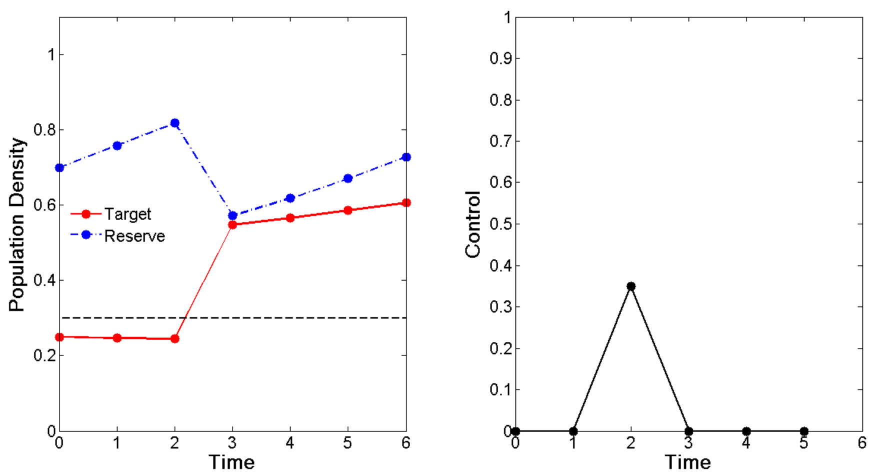


Figure 4.7: Simulation for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.30$, $s = 0.70$, $p = 1.00$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 0.00$, $A_2 = 0.70$, $B = 0.25$, with $h = 0.05$. The left graph shows the density of the target (red) and reserve (blue dashed) populations at each time step. The right graph shows the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control in this simulation are $u = [0.00\ 0.00\ 0.35\ 0.00\ 0.00\ 0.00]$.

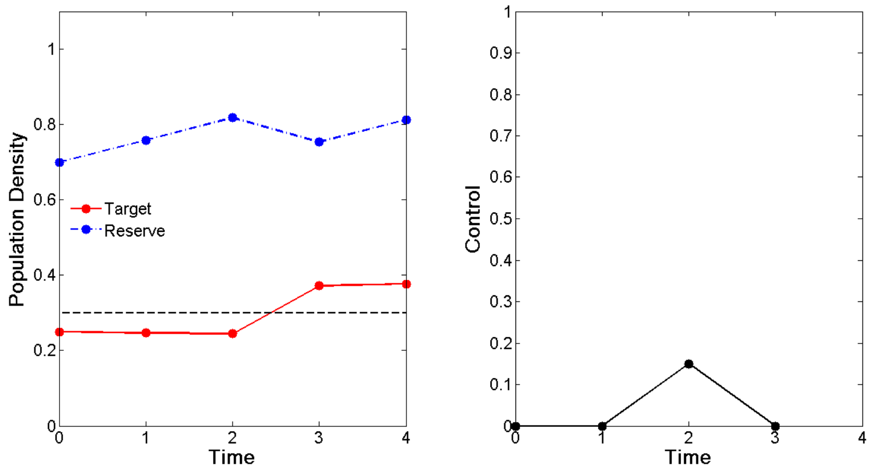


Figure 4.8: Simulation for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.30$, $s = 0.70$, $p = 1.00$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 0.00$, $A_2 = 0.70$, $B = 0.25$, with $h = 0.05$. The left graph shows the density of the target (red) and reserve (blue dashed) populations at each time step. The right graph shows the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control in this simulation are $u = [0.00\ 0.00\ 0.15\ 0.00]$.

qualitative strategy (augment at only time step $k = 2$), though a slightly larger proprortion of the reserve population is translocated to the target population in this scenario when $T = 5$.

Next, we examine what occurs when the time horizon is shortened. In this scenario we let $s = 0.7$, $p = 1$, $A_1 = 0.10$, $A_2 = 0.70$, $B = 0.25$, and $T = 4$. The results for this scenario are shown in Figure 4.8. Note the value for the optimal control in this scenario is

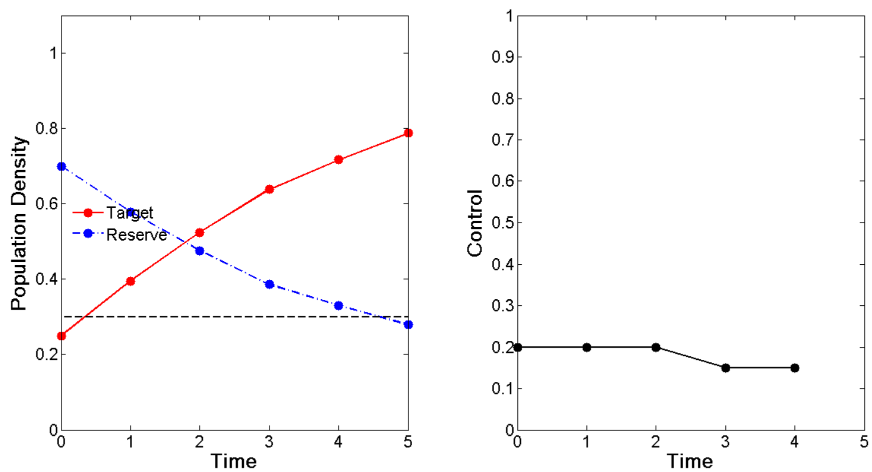
$$u = [0.00\ 0.00\ 0.15\ 0.00],$$

and thus the only augmentation occurs at time step $k = 2$ when 15% of the reserve population is translocated to the target population. Comparing to the similar scenario where $T = 5$ (see Figure 4.2), we see the same qualitative strategy (augment at only time step $k = 2$), though a smaller proprortion of the reserve population is translocation to the target population in this scneario when $T = 4$.

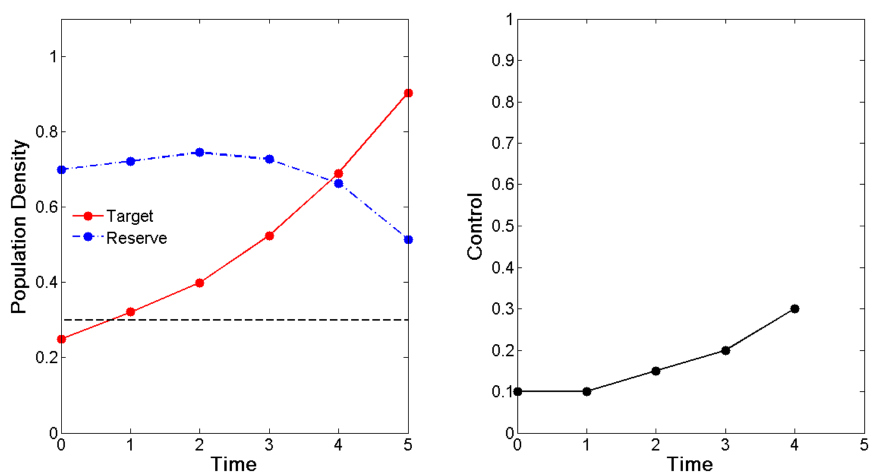
4.4.4 Varying the Intrinsic Growth Rate of the Reserve Population

Next, we consider the impact of varying the intrinsic growth rate of the reserve population, s. In the these scenarios we take $p = 1.00$, $A_1 = 1$, and $A_2 = 0$ so that these results may be compared to results from the continuous time optimal control formulations in Chapter 2 using similar parameter sets.

In the first scenario we take $s = 0.3$, and $B = 0$ (see Figure 4.9(a))), and in the second scenario we take $s = 1.2$ and $B = 0$ (see Figure 4.9(b)). Since $B = 0$ in each case, no



(a) Lower intrinsic growth rate, $s = 0.3$.



(b) Higher intrinsic growth rate, $s = 1.2$.

Figure 4.9: Simulation for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.25$, $p = 1$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 1$, $A_2 = 0$, $B = 0$, with $h = 0.05$. In (a) $s = 0.3$ and in (b) $s = 1.2$. The graphs on the left show the density of the target (red) and reserve (blue dashed) populations at each time step. The graphs on the right show the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control are (a) $u = [0.20\ 0.20\ 0.20\ 0.15\ 0.15]$, and (b) $u = [0.10\ 0.10\ 0.15\ 0.20\ 0.30]$.

importance is given to maximizing the reserve population at the final time. In Figure 4.9(a) the optimal augmentation strategy is

$$u = [0.20\ 0.20\ 0.20\ 0.15\ 0.15],$$

that is, at time steps $k = 0, 1, 2$ translocate 20% of the reserve population to the target population, and at time steps $k = 3, 4$, translocate 15%. In Figure 4.9(b), the optimal augmentation strategy is

$$u = [0.10\ 0.10\ 0.15\ 0.20\ 0.30],$$

that is, at time steps $k = 0, 1$, translocate 10% of the reserve population to the target population, at time step $k = 2, 3, 4$ translocated 15%, 20%, and 30%, respectively. Notice when $s = 0.3$ in Figure 4.9(a), the reserve population is being harvested such that by the final time, the reserve population is below its minimunm threshold for growth, $b = 0.3$ (see black dashed line in Figure 4.9(a)). This is not the case when $s = 1.2$ in Figure 4.9(b). In the scenario in Figure 4.9(a), since the intrinsic growth rate is so low, the reserve population cannot replenish itself quickly enough to compensate for the individuals being harvested from the population for the augmentation. In the scenario in Figure 4.9(b), when s is much higher, the reserve population is able to reproduce quickly enough to replace the individuals being harvested. Note that these results are roughly qualitatively similar to the continuous time scenario with similar parameters shown in Chapter 2 in Figure 2.4.

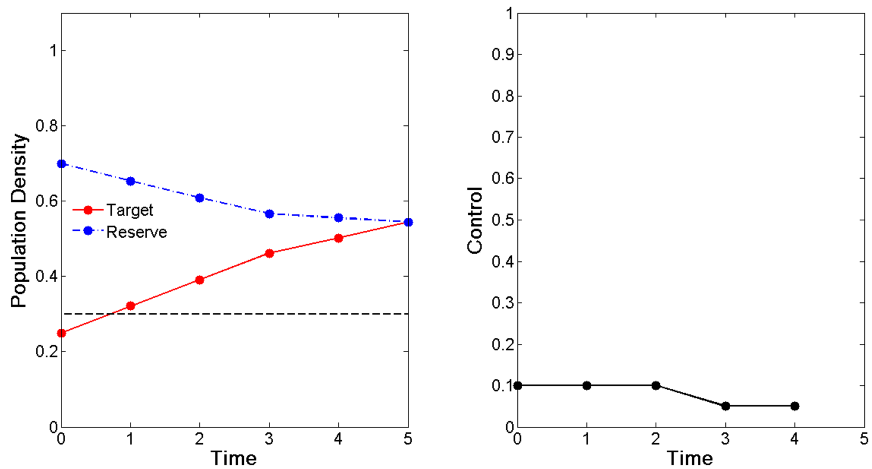
We can counteract the problem of over-harvesting the reserve population by increasing the value B. Thus, in the first of the next two scenarios, we take $s = 0.3$ and $B = 0.75$ (see Figure 4.10(a)), and in the second of the two scenarios we take $s = 1.2$ and $B = 0.75$ (see Figure 4.10(b)). Since $B = 0.75$ in each case it is 75% as important to maximize the reserve population at the final time as it is to maximize the target population at the final time. In Figure 4.10(a) the optimal augmentation strategy is

$$u = [0.10\ 0.10\ 0.10\ 0.05\ 0.05],$$

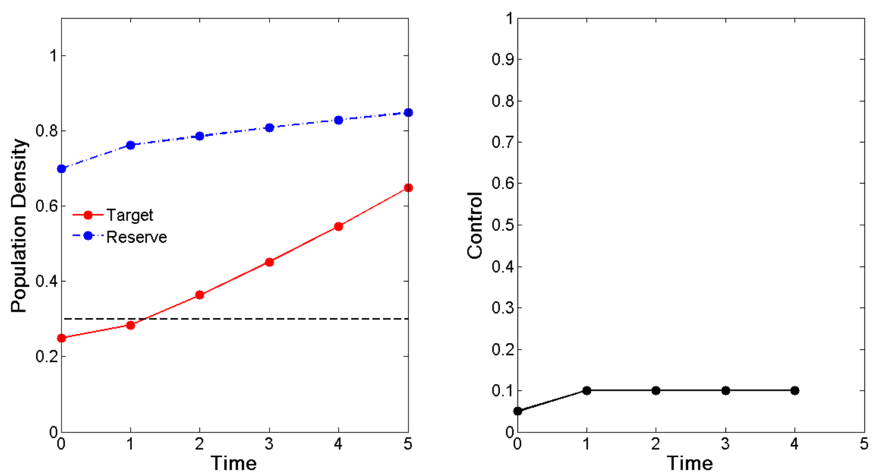
that is, at time steps $k = 0, 1, 2$, translocate 10% of the reserve population to the target population, and at time steps $k = 3, 4$, translocate 5% of the reserve population. In Figure 4.10(b), the optimal augmentation strategy is

$$u = [0.05\ 0.10\ 0.10\ 0.10\ 0.10],$$

that is, at time step $k = 0$, translocate 5% of the reserve population to the target population, then translocate 10% at each of the remaining time steps. Notice when $s = 0.3$ in Figure 4.10(a) the reserve population is being harvested in such a way that the population remains above its minimum threshold for growth, $b = 0.3$ (see black dashed line in 4.10(a)), for the entire time horizon. Since the importance of maximizing the reserve population at the final time increased (as compared with the scenario in 4.9(a) where $B = 0$), less individuals are being harvested from the reserve population, and the reserve population is able to



(a) Lower intrinsic growth rate, $s = 0.3$.



(b) Higher intrinsic growth rate, $s = 1.2$.

Figure 4.10: Simulation for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.25$, $p = 1$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 1$, $A_2 = 0$, $B = 0.75$, with $h = 0.05$. In (a) $s = 0.3$ and in (b) $s = 1.2$. The graphs on the left show the density of the target (red) and reserve (blue dashed) populations at each time step. The graphs on the right show the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control are (a) $u = [0.10\ 0.10\ 0.10\ 0.05\ 0.05]$, and (b) $u = [0.05\ 0.10\ 0.10\ 0.10\ 0.10]$.

reproduce quickly enough to replace the individuals that are removed. Note that these results are roughly qualitatively similar to to the continuous time scenario with similar parameters shown in Chapter 2 in Figure 2.5.

4.4.5 Varying the Ratio of the Reserve Carrying Capacity to the Target Carrying Capacity

Lastly, we examine the impact of varying the ratio of the reserve population carrying capacity to the target population carrying capacity, p. When $p < 1$, the reserve carrying capacity is smaller than the target carrying capacity. Thus, $p = 0.5$ could represent when the reserve population is generated from a captive breeding program or zoo population. When $p > 1$, the reserve carrying capacity is larger than the target carrying capacity. Thus, $p = 1.2$ could represent when the reserve population is a wild, stable (and possibly protected) population. In the first two scenarios, we let $s = 1.2$, $A_1 = 1$, $A_2 = 0$, and $B = 0$ so that these results may be compared to results from the continuous time optimal control formulation in Chapter 2 using similar parameter sets. Since $B = 0$ no importance is given to maximizing the reserve population at the final time.

In the first of these two scenarios, we take $p = 0.50$. The results for this scenario are shown in Figure 4.11. Note that the values for the optimal control in this scenario are

$$u = [0.10\ 0.15\ 0.15\ 0.15\ 0.20],$$

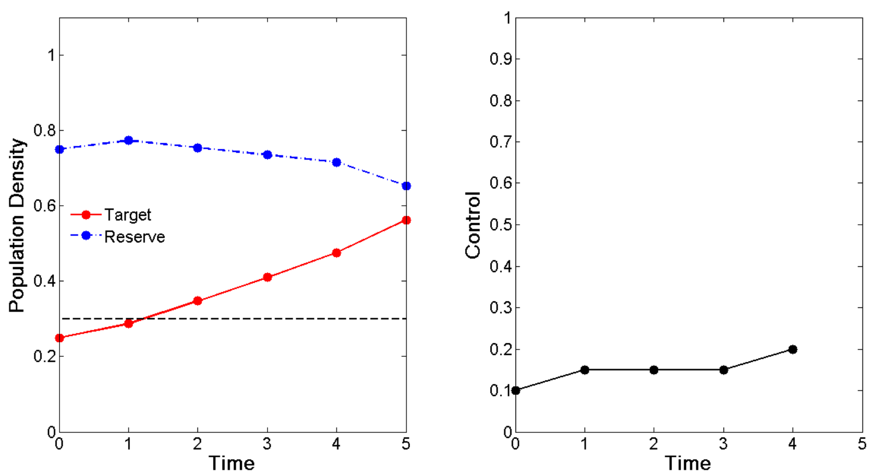


Figure 4.11: Simulation for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.25$, $s = 1.2$, $p = 0.50$, $x_0 = 0.25$, $y_0 = 0.75$, $A_1 = 1$, $A_2 = 0$, $B = 0$, with $h = 0.05$. The left graph shows the density of the target (red) and reserve (blue dashed) populations at each time step. The right graph shows the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control in this simulation are $u = [0.10\ 0.15\ 0.15\ 0.15\ 0.20]$.

thus there is a low level of augmentation occurring at each time step. At time step $k = 0$, 10% of the reserve population is translocated to the target population, at time steps $k = 1, 2, 3$, 15% of the reserve population is translocated, and at time step $k = 4$, 20% of the reserve population is translocated. Notice, in this scenario, that though the proportion of the reserve population being translocated to the target population at each time step is low (20% or less), by the final time the target population is well above its minimum threshold for growth, $a = 0.3$ (see the dashed black line in Figure 4.11). Additionally, the reserve population is harvested in such a way that it remains above its minimum threshold for growth at the final time, i.e. $y_T > b = 0.3$ (see the dashed black line in Figure 4.11). A similar qualitative result was seen for a similar parameter set in the continuous time case in Chapter 2 (see Figure 2.6 where the dash-dot line corresponds to $p = 0.5$).

In the next scenario, we take $p = 1.2$. The results for this scenario are shown in Figure 4.12. Note that the value for the optimal control in this scenario are

$$u = [0.10\ 0.15\ 0.15\ 0.20\ 0.30].$$

Here, we see a low level of augmentation occurring until the last time step for augmentation where a moderate proportion of the reserve population is translocated into the target population. At time step $k = 0$, 10% of the reserve population is translocated into the target population, at time steps $k = 1, 2$, 15% of the reserve population is translocated, at time step $k = 3$, 20% is translocated, and at $k = 4$, 30% is translocated. The optimal

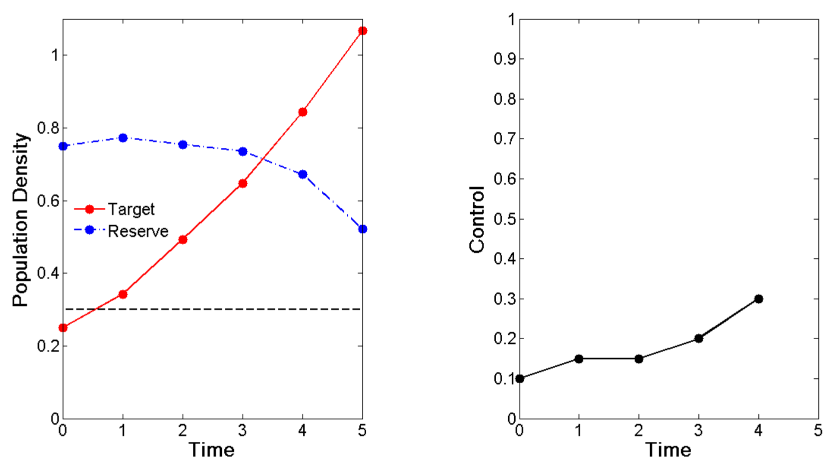


Figure 4.12: Simulation for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.25$, $s = 1.2$, $p = 1.2$, $x_0 = 0.25$, $y_0 = 0.75$, $A_1 = 1$, $A_2 = 0$, $B = 0$, with $h = 0.05$. The left graph shows the density of the target (red) and reserve (blue dashed) populations at each time step. The right graph shows the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control in this simulation are $u = [0.10\ 0.15\ 0.15\ 0.20\ 0.30]$.

augmentation strategy in this scenario is qualitatively similar to the augmentation strategy in the scenario shown in Figure 4.11.

Notice, in this scenario, the target population is augmented in such a way that it rises above its carrying capacity by the final time, i.e. $x_T > 1$. Since $p > 1$, the carrying capacity of the reserve population is higher than that of the target population. Thus, though the proportions of the reserve population are low, as in the scenario in Figure 4.11, the actual number of individuals being translocated is higher in this scenario than in the scenario in Figure 4.11. Additionally, the reserve population is harvested in such a way that it remains above its minimum threshold for growth at the final time, i.e. $y_T > b = 0.3$ (see the dashed black line in Figure 4.12).

In the next two scenarios we take $s = 1.2$, $A_1 = 0$, $A_2 = 0.001$, $B = 0$. Again, since $B = 0$ in each case, no importance is given to maximizing the reserve population. Notice that the linear cost coefficient is considerably smaller than what we have considered in previous cases. Additionally, note that though taking $A_1 = 0$ makes the objective functional linear with respect to the control, the underlying state equations retain their nonlinearity with respect to the control.

In the first of these two scenarios we take $p = 0.5$ (see Figure 4.13(a)), and in the second of these scenario we take $p = 1.2$ (see Figure 4.13(a)). Note that in Figure 4.13(a) the optimal control is

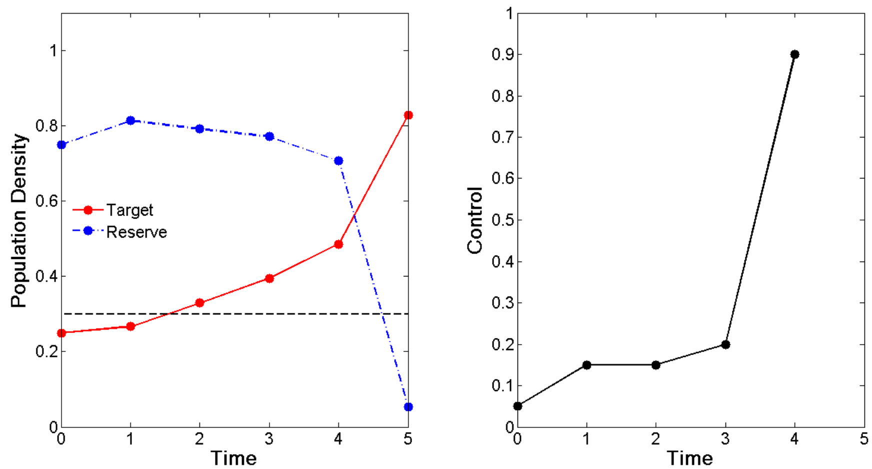
$$u = [0.05\ 0.15\ 0.15\ 0.20\ 0.90],$$

while in Figure 4.13(b) the optimal control is

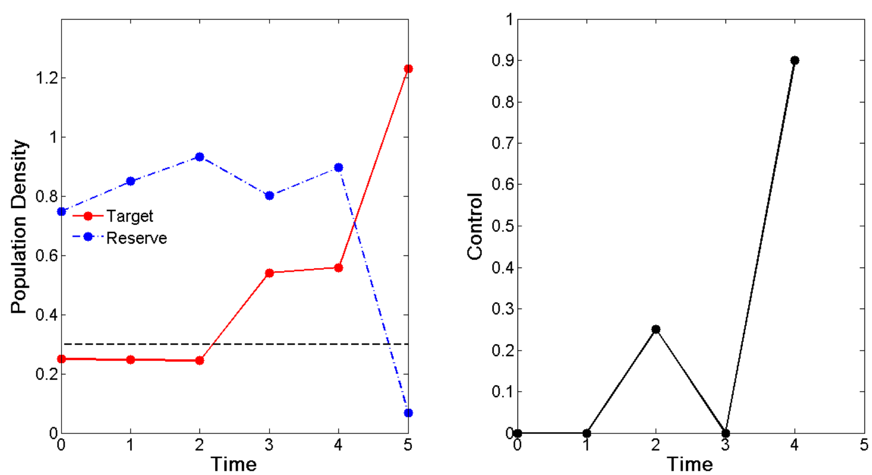
$$u = [0.00\ 0.00\ 0.25\ 0.00\ 0.90].$$

These two different augmentation strategies are qualitatively different. The optimal augmentation in Figure 4.13(a) maintains a low level of augmentation at each time step until the last time step when it switches to translocating the maximum allowable proportion of the reserve population to the target population. The optimal augmentation strategy in Figure 4.13(b), on the other hand, only translocated individuals from the reserve population to the target population at two time steps: 25% at time step $k = 2$, and 90% (the maximum allowable proportion) at time step $k = 4$. If we compare these scenarios to the scenarios in Figure 4.11 ($p = 0.5$, $A_1 = 1$, $A_2 = 0$, and $B = 0$) and Figures 4.12 ($p = 1.2$, $A_1 = 1$, $A_2 = 0$, and $B = 0$), we see those two scenarios (Figures 4.11 and 4.12) have the same qualitative strategy, while these two scenarios (Figure 4.13) differ qualitatively.

Furthermore, if we compare these two scenarios (Figure 4.13) to those scenarios that use the continuous time optimal control formulation with similar parameters in Chapter 3 (see Figure 3.3), we see that qualitatively the optimal augmentation strategies differ greatly. However, this should not be surprising. Though taking $A_1 = 0$ in these two discrete scenarios (Figure 4.13) makes the objective functional (and the translocation cost) linear with respect to the control, the underlying state variables are still nonlinear with respect to the control. In the continuous model presented in Chapter 3, the state variables are already



(a) Lower ratio of carrying capacities, $p = 0.5$.



(b) Higher ratio of carrying capacities, $p = 1.2$.

Figure 4.13: Simulation for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.25$, $s = 1.2$, $x_0 = 0.25$, $y_0 = 0.75$, $A_1 = 0$, $A_2 = 0.001$, $B = 0$, with $h = 0.05$. In (a) $p = 0.5$ and in (b) $p = 1.2$. The graphs on the left show the density of the target (red) and reserve (blue dashed) populations at each time step. The graphs on the right show the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control are (a) $u = [0.05\ 0.15\ 0.15\ 0.20\ 0.90]$, and (b) $u = [0.00\ 0.00\ 0.25\ 0.00\ 0.90]$.

linear with respect to the control, and when $A_1 = 0$ the objective functional is linear with respect to the control. This difference in the state variables' dependence on the control, accounts for the qualitative differences we find between the resulting optimal augmentation strategies in discrete and continuous models.

4.5 Conclusions

In this chapter we explored an optimal control formulation for species augmentation which utilizes a discrete time difference equation model to describe the dynamics of the target and reserve populations. For the discrete model in this chapter we assume the order of events at each time step is that the population is augmented before it grows (via natural reproduction). The resulting difference equations were cubic with respect to the control, u (see Equations 4.5 and 4.6), and the Hamiltonian, H_k, constructed from the state equations and objective functional did not satisfy the concavity condition $\frac{\partial^2 H_k}{\partial u_k^2} \leq 0$ for all time steps k and all possible parameter sets. Thus, we resorted to a numerical method that directly maximized the objective functional (see Section 4.3). In Section 4.4 we explored the numerical results for several different illustrative parameter sets.

Several important conclusions about the discrete control of species augmentation can be drawn from the numerical results for these illustrative parameters sets. First, in Sections 4.4.1 and 4.4.2, we observed that natural resource managers planning augmentations may need to increase importance of maximizing the reserve population at the final time in order to maintain the reserve population above its minimum threshold for growth (compare Figures 4.1 and 4.2). Additionally, we observed that if the cost of augmentation is lowered, it is optimal to move a higher proportion of the reserve population into the target population and possibly wait longer (see Figures 4.2, 4.3). Similarly, we observed that if the cost of augmentation increases, it is optimal to translocate a smaller proportion of the reserve population to the target population (see Figures 4.2 and 4.4). However, if the cost of augmentation increases too high, the optimal solution may be to do nothing (see Figure 4.5). These results make intuitive sense that when translocation is less expensive resource managers can move more individuals and when translocation is more expensive resource managers can move fewer individuals. However, this model tells us exactly how many more or less to translocate and maintain an optimal outcome when costs are increased or lowered.

Next, in Section 4.4.3, we observed when the time horizon of an augmentation project changes, though the optimal time to augment may not change, the optimal proportion of the reserve population to translocate to the target population at that time will change. In our examples, the optimal proportion of the reserve population to translocate will decrease if the time horizon shortens and increase if the time horizon increases (see Figures 4.2, 4.7, and 4.8). These results might seem counter-intuitive. One might hypothesize that given a shorter time horizon, a resource manager would need to augment with a larger proportion of the reserve population at time step $k = 2$ to maximize the target population at the final time. However, recall that we are optimizing the objective functional which balances maximizing the target and reserve populations at the final time with the cost of augmentation. Moving a larger proportion of the reserve population at time step $k = 2$ will cause the target population to be higher at the final time, but it will also increase the cost (which we are trying to minimize), and lower the size of the reserve population at the final time (which we are trying to maximize) since the reserve population does not have as long of a time horizon to replace the individuals who were harvested. We can think about increasing the time horizon in a similar fashion.

It should be noted, that due to the numerical method used, we were limited in how far we could expand the time horizon. Setting $T > 6$ resulted in a problem that required too computationally large to solve on the machines we used. Further investigations of extending the time horizon is needed in order to gain a broader understanding of the impact this has on the optimal augmentation strategy. However, a more efficient method for determining the optimal control is needed if we are to consider further expanding the time horizon.

In Section 4.4.4, we observed that a low intrinsic growth rate of the reserve population combined with no importance given to maximizing the reserve population at the final time leads to a scenario where there reserve population is harvested such that if falls below its minimum threshold for growth by the final time (see Figure 4.9). We observed this same phenomenon in Chapter 2 (see Figure 2.4) and in Chapter 3 (see Figure 3.1). As in Chapters 2 and 3, we saw that by increasing the importance of maximizing the reserve population at the final time, i.e. increasing the value of B, we can ensure that the reserve population remains above its minimum threshold for growth. Thus, again we see that it is important for resource managers planning augmentation to consider the importance of maintaining the reserve population. The trade-off when increasing the value of B is that the target population is not quite as large by the final time. However, in the simulations we explored the target population was still able to rise above its minimum threshold for growth by the final time despite the increase in B (compare Figures 4.9 and 4.10).

In Section 4.4.5, we considered the effects of different ratios of the reserve carrying capacity to the target carrying capacity. We let $p = 0.5$ to represent a population whose reserve carrying capacity is smaller than the target populations carrying capacity, and $p = 1.2$ to represent a population whose reserve carrying capacity is larger than the target carrying capacity. It is important to note that when comparing optimal augmentation strategies where $p \neq 1$, the actual proportion of individuals being translocated from the reserve population to the target population needs to be adjusted by the ratio p to account for the difference in the effects on the target population densities. Thus, in comparing Figure 4.11 and Figure 4.12, even though the proportions translocated at each time step are similarly low in each scenario, the actual number of individuals being translocated when $p > 1$ is greater than the number translocated when $p < 1$. Thus, though the optimal augmentation strategies for the scenarios in Figures 4.11 and 4.12 are somewhat qualitatively similar, the effect on the corresponding target and reserve states is very different. Therefore, when natural resource managers are planning species augmentations, in order to accurately predict the impact of an augmentation strategy on both the target and reserve population it is important that the ratio of the two populations' carrying capacities is taken into account.

Additionally, in Section 4.4.5, we considered two scenarios which we could compare to scenarios with the same parameters in Chapter 3. These scenarios took $A_1 = 0$, $A_2 = 0.001$, and $B = 0$ with $p = 0.5$ in Figure 4.13(a) and $p = 1.2$ in Figure 4.13(b). When compared to the scenarios with the same parameters in Chapter 3, we observed that the qualitative augmentation strategies differed greatly. However, we did not expect the qualitative augmentation strategies to necessarily be similar, due to the difference in the discrete and continuous models' dependence on the control in the state equations. In this discrete model, though taking $A_1 = 0$ makes the objective functional linear with respect to the control, the underlying state variables remain nonlinear with respect to the control. However, in the continuous model in Chapter 3, the state equations are already linear with respect to the control and taking $A_1 = 0$ makes the objective functional linear with respect to the control. This difference in the state variables' dependence on the control, highlights the differences that can arise between choosing a model with continuous time growth and a model with discrete time growth.

Iin the scenarios shown in Sections 4.4.1 - 4.4.3, the dominating term of the cost of translocation is the linear term. The cost coefficient for the quadratic term is taken as either $A_1 = 0$ or $A_1 = 0.1$, whereas the cost coefficient for the linear term, A_2, was set between 0.5 and 0.9. It is interesting to note, that in each of these parameter scenarios, the optimal augmentation strategy was to augment at only one time step (see Figures 4.1 - 4.8), or to do no augmentation at all (this was the case when $A_1 = 0.1$ and $A_2 = 0.9$). This is very different from the continuous time control scenarios explored in Chapters 2 and 3. In Chapter 2 the optimal augmentation strategies always maintained continual augmentation at all times, even if only at low rates. In Chapter 3 the optimal augmentation strategies switched between no augmentation over time periods and maximum augmentation effort over time periods. Note that we did see some discrete time scenarios where the optimal augmentation strategy maintains some level of augmentation for every time step (see Figures 4.9(a) - 4.13(a)). These strategies were optimal when $A_1 = 1$ and $A_2 = 0$, and when $A_1 = 0$, $A_2 = 0.001$, and $p = 0.5$. These drastic differences in the types of qualitative optimal augmentation strategies that occur highlight the difference between assuming continuous time growth with the ability for continuous time augmentation, and discrete time growth with discrete time augmentations. For natural resource managers who are planning augmentations for various species, the optimal strategy given by the discrete model is certainly more easily implemented.

Lastly, recall that in this optimal control formulation, the underlying population dynamics were modeled by discrete time models which determined the population *density* of both the target and reserve populations at each time step. Due to the fact that we model population densities, we could ignore issues that arise in discrete modeling with counting fractional individuals. However, to implement the optimal augmentation strategies found using this model in practice, we must consider how to deal with fractional individuals.

Suppose we have the scenario shown in Figure 4.4 where the carrying capacity of both the target and reserve populations is 100 individuals. Then the optimal augmentation strategy is to move 15% of the reserve population at time step $k = 2$. At time step $k = 2$, the reserve population is at 81.76% of its carrying capacity. Thus, the optimal control strategy tell us to translocate $100 \times 0.8176 \times 0.15 = 12.264$ individuals from the reserve population to the target population at time step $k = 2$. Clearly, a natural resource manager cannot move 0.264 of an inidividual. Thus, a decision must be made here whether to round up or down. If we round down, then fewer individuals are moved to the target population and in some scenarios this could affect whether the target population is able to rise above its minimum threshold for growth by the final time. If we round up, then more individuals are removed from the reserve population and in some scenarios this could result in the reserve population falling belows its minimum threshold for growth by the final time.

Chapter 5

Discrete Time Model (Grow then Augment)

In Chapter 4 we considered the discrete time augmentation model where the population can be augmented before the growing season each year. Now we continue to investigate the effects of the order of events, and consider the case where augmentation occurs after the natural population growth. The underlying population model (in the absence of human intervention) is

$$N_{k+1} - N_k = rN_k\left(\frac{N_k}{K_N} - a\right)\left(1 - \frac{N_k}{K_N}\right), \tag{5.1}$$

$$R_{k+1} - R_k = sR_k\left(\frac{R_k}{K_R} - b\right)\left(1 - \frac{R_k}{K_R}\right) \tag{5.2}$$

where N_k and R_k are the target and reserve population sizes at time step k, r and s are the intrinsic growth rates of N and R, respectively, and K_N and K_R are the carrying capacities of N and R, respectively. The model is constructed so for $N_k < aK_N$ and $R_k < bK_R$ the endangered and reserve populations, respectively, are declining.

In this chapter, we explore this model when the population can be augmented after the growth in each time step. That is, if first we let the populations grow and then harvest and augment, the system in Equations (5.1-5.2) becomes

$$\begin{aligned} N_{k+1} &= N_k\left[r\left(\frac{N_k}{K_N} - a\right)\left(1 - \frac{N_k}{K_N}\right) + 1\right] \\ &\quad + u_k R_k\left[s\left(\frac{R_k}{K_R} - b\right)\left(1 - \frac{R_k}{K_R}\right) + 1\right], \end{aligned} \tag{5.3}$$

$$R_{k+1} = (1 - u_k)R_k\left[s\left(\frac{R_k}{K_R} - b\right)\left(1 - \frac{R_k}{K_R}\right) + 1\right]. \tag{5.4}$$

Rescaling these two populations with respect to their carrying capacities ($x_k \equiv \frac{N_k}{K_N}$ and $y_k \equiv \frac{R_k}{K_R}$) gives

$$x_{k+1} = x_k \left[r \left(x_k - a \right) \left(1 - x_k \right) + 1 \right] + p u_k y_k \left[s \left(y_k - b \right) \left(1 - y_k \right) + 1 \right], \tag{5.5}$$

$$y_{k+1} = \left(1 - u_k \right) y_k \left[s \left(y_k - b \right) \left(1 - y_k \right) + 1 \right]. \tag{5.6}$$

where $p \equiv K_R/K_N$, i.e. the ratio of the reserve carrying capacity to the endangered carrying capacity. We assume that the target population x has an initial density x_0 below its minimum threshold for growth a, and that the reserve population y has an initial density y_0 above its minimum threshold for growth b, i.e. $x_0 < a$ and $y_0 > b$. Thus, the optimal control formulation is

$$\max_{u \in U} \left[x_T + B y_T - \sum_{n=0}^{T-1} \left(A_1 u_n^2 + A_2 u_n \right) \right] \tag{5.7}$$

$$x_{k+1} = x_k \left[r \left(x_k - a \right) \left(1 - x_k \right) + 1 \right] + p u_k y_k \left[s \left(y_k - b \right) \left(1 - y_k \right) + 1 \right], x_0 < a \tag{5.8}$$

$$y_{k+1} = \left(1 - u_k \right) y_k \left[s \left(y_k - b \right) \left(1 - y_k \right) + 1 \right], y_0 > b, \tag{5.9}$$

where $k = 0, 1, \ldots, T-1$. We refer to the function being maximized as the objective functional, denoted

$$J(u) = x_T + B y_T - \sum_{n=0}^{T-1} \left(A_1 u_n^2 + A_2 u_n \right). \tag{5.10}$$

Using this objective functional, we are maximizing the target population at the final time, maximizing the reserve population at the final time (but weighted by the constant $0 < B < 1$), and minimizing the cost associated with translocated individuals from the reserve population to the target population over the time steps $(0, 1, \ldots, T-1)$. The cost term $A_1 u_k^2$, which has quadratic dependence on u_k, accounts for nonlinear increases in the costs of translocation as the fraction translocated at a given time step increases. The cost term $A_2 u_k$, which has linear dependence on u_k, accounts for linear increases in the costs of translocation as the fraction translocated at a given time step increases. Note that we assume $A_1 > 0$ and $A_2 \geq 0$.

5.1 Characterization of an Optimal Control

Since the Hamiltonian for this problem does have convexity with respect to the control, we are able to use Pontryagin's Maximum Principle for optimal control using discrete difference equations to derive a characterization for an optimal control. The following theorem assume that there exists an optimal control, which is valid since we have bounded controls and states for a finite number of time steps.

Theorem 5.1.1. *Suppose* $u^* = \left(u_0^*, u_1^*, \ldots, u_{T-1}^*\right)$ *is an optimal control vector at each time step* k *for the optimal control formulation given in Equations (5.7)-(5.9). Let* $x^* = (x_0^*, x_1^*, \ldots, x_T^*)$ *and* $y^* = (y_0^*, y_1^*, \ldots, y_T^*)$ *be the corresponding state solutions. Then there exists adjoint variables* $\lambda_x = (\lambda_{x,0}, \lambda_{x,1}, \ldots, \lambda_{x,T})$ *and* $\lambda_y = (\lambda_{y,0}, \lambda_{y,1}, \ldots, \lambda_{y,T})$ *such that*

$$\lambda_{x,k} = \lambda_{x,k+1}\left[-3r\left(x_k^*\right)^2 + 2r(1+a)x_k^* + (1-ra)\right], \tag{5.11}$$

$$\lambda_{x,T} = 1, \tag{5.12}$$

$$\lambda_{y,k} = \left[pu_k^*\lambda_{x,k+1} + (1-u_k^*)\lambda_{y,k+1}\right]\left[-3s\left(y_k^*\right)^2 + 2s(1+b)y_k^* + (1-sb)\right], \tag{5.13}$$

$$\lambda_{y,T} = B. \tag{5.14}$$

Furthermore, the optimal control is represented by

$$u_k^* = \min\left\{1, \max\left\{0, \frac{-A_2 + (p\lambda_{x,k+1} - \lambda_{y,k+1})\left[sy_k(y_k-b)(1-y_k) + y_k\right]}{2A_1}\right\}\right\}. \tag{5.15}$$

Proof: Suppose $u^* = \left(u_0^*, u_1^*, \ldots, u_{T-1}^*\right)$ is an vector of optimal controls with corresponding states $x^* = (x_0^*, x_1^*, \ldots, x_T^*)$ and $y^* = (y_0^*, y_1^*, \ldots, y_T^*)$. Using Pontryagin's Maximum Principle for optimal control formulations with discrete time difference state equations [39, 44], the Hamiltonian is formed

$$\begin{aligned} H_k = & -A_1u_k^2 - A_2u_k \\ & + \lambda_{x,k+1}\left\{x_k\left[r(x_k-a)(1-x_k)+1\right] + pu_ky_k\left[s(y_k-b)(1-y_k)+1\right]\right\} \\ & + \lambda_{y,k+1}\left\{(1-u_k)y_k\left[s(y_k-b)(1-y_k)+1\right]\right\} \end{aligned} \tag{5.16}$$

and the adjoint equations are constructed

$$\begin{aligned} \lambda_{x,k} &= \frac{\partial H_k}{\partial x_k} = \lambda_{x,k+1}\left\{-3r(x_k^*)^2 + 2r(1+a)x_k + (1-ra)\right\} \\ \lambda_{y,k} &= \frac{\partial H_k}{\partial y_k} = \left[pu_k^*\lambda_{x,k+1} + (1-u_k^*)\lambda_{y,k+1}\right]\left\{-3sy_k^2 + 2s(1+b)y_k + (1-sb)\right\}, \end{aligned}$$

and the transversality condition gives $\lambda_{x,T} = 1$ and $\lambda_{y,T} = B$. The Hamiltonian differentiated with respect to the control is

$$\frac{\partial H_k}{\partial u_k} = -2A_1u_k - A_2 + (p\lambda_{x,k+1} - \lambda_{y,k+1})\,y_k\left[s(y_k-b)(1-y_k)+1\right]. \tag{5.17}$$

For the given objective functional, we maximize the Hamiltonian with respect to u_k.

On the set $\{k | 0 < u_k^* < 1\}$, $\frac{\partial H_k}{\partial u_k} = 0$ at u_k^*. Thus,

$$\begin{aligned}\frac{\partial H_k}{\partial u_k} &= -2A_1 u_k - A_2 + (p\lambda_{x,k+1} - \lambda_{y,k+1})\, y_k \left[s(y_k - b)(1 - y_k) + 1\right] = 0 \\ \Rightarrow u_k^* &= \frac{-A_2 + (p\lambda_{x,k+1} - \lambda_{y,k+1})\, y_k \left[s(y_k - b)(1 - y_k) + 1\right]}{2A_1}.\end{aligned}$$

When $\frac{\partial H_k}{\partial u_k} < 0$, then $u_k^* = 0$ and

$$\begin{aligned}-A_2 + (p\lambda_{x,k+1} - \lambda_{y,k+1})\, y_k \left[s(y_k - b)(1 - y_k) + 1\right] &< 0 \\ \Rightarrow \frac{-A_2 + (p\lambda_{x,k+1} - \lambda_{y,k+1})\, y_k \left[s(y_k - b)(1 - y_k) + 1\right]}{2A_1} &< 0\end{aligned}$$

since $A_1 > 0$.

When $\frac{\partial H_k}{\partial u_k} > 0$, then $u_k^* = 1$ and

$$\begin{aligned}-2A_1 - A_2 + (p\lambda_{x,k+1} - \lambda_{y,k+1})\, y_k \left[s(y_k - b)(1 - y_k) + 1\right] &> 0 \\ \Rightarrow \frac{-A_2 + (p\lambda_{x,k+1} - \lambda_{y,k+1})\, y_k \left[s(y_k - b)(1 - y_k) + 1\right]}{2A_1} &> 1.\end{aligned}$$

Combining the cases when $u_k^* = 0$, $0 < u_k^* < 1$, and $u_k^* = 1$, we find the characterization of optimal control is

$$u_k^* = \min\left\{1, \max\left\{0, \frac{-A_2 + (p\lambda_{x,k+1} - \lambda_{y,k+1})\left[s y_k (y_k - b)(1 - y_k) + y_k\right]}{2A_1}\right\}\right\}.$$

■

5.2 Numerical Methods

The optimal control can be numerically calculated under various parameter sets using a discrete time version of the forward-backward sweep method which we first described in Section 2.3. An initial guess is made for the vector of optimal controls, $u = (u_0, u_1, \ldots, u_{T-1})$. Using the initial guess for u, we then solve for $x = (x_0, x_1, \ldots, x_T)$ and $y = (y_0, y_1, \ldots, y_T)$ using Equations (5.8) and (5.9) and the given initial conditions x_0 and y_0. Then, using the vectors u, x, and y, we solve for $\lambda_x = (\lambda_{x,0}, \lambda_{x,1}, \ldots, \lambda_{x,T})$ and $\lambda_y = (\lambda_{y,0}, \lambda_{y,1}, \ldots, \lambda_{y,T})$ using Equations (5.11) and (5.13) with transversality conditions $\lambda_{x,T} = 1$ and $\lambda_{y,T} = B$. At this point, the optimal control us updated using the characterization for the optimal control, Equation (5.15), and the vectors for the state and adjoint variables. This updated control replaces the initial control and the process is repeated until the successive iterates of control vectors are sufficiently close.

5.3 Numerical Results

In considering various parameter scenarios, the parameter constrains on x_0 and y_0, $x_0 < a$ and $y_0 < b$, must be included. For the examples included here, we take the minimum threshold for growth for both the target and reserve populations to be 0.3 (that is 30% of each populations' carrying capacity), and $x_0 = 0.25$. In serveral of the scenarios $y_0 = 0.70$ and in a few of the scenarios $y_0 = 0.75$. Thus, the target population is starting just below its minimum threshold for growth, and the reserve population is starting well above its minimum threshold for growth. Here we are looking for qualitative results, and thus the optimal values for u_k are rounded to the nearest one-hundreth. That is, we are only interested in accuarcy down to 1% of the population. Unless otherwise stated, the final time is $T = 5$.

5.3.1 Varying the Cost of Translocation

In the first set of scenarios we consider varying the cost of translocation by varying A_2. In the next four scenarios, we take $a = 0.30$, $b = 0.30$, $r = 0.30$, $s = 0.70$, $p = 1$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 0.1$ and vary A_2 and B.

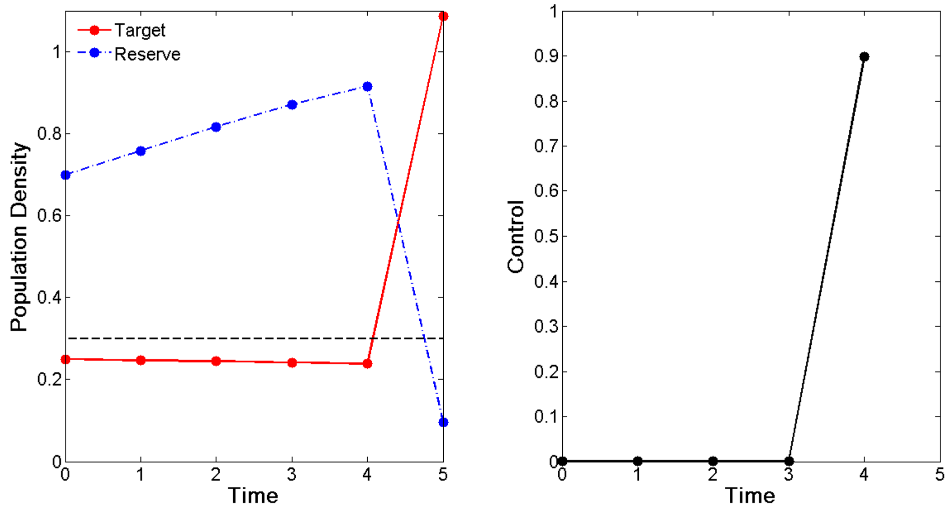
In the first scenario, we let $A_2 = 0.7$ and $B = 0$ (see Figure 5.1(a)). Thus, no importance is given to maximizing the reserve population at the final time. The values for the optimal control in this scenario are

$$u = [0.00\ 0.00\ 0.00\ 0.00\ 0.90],$$

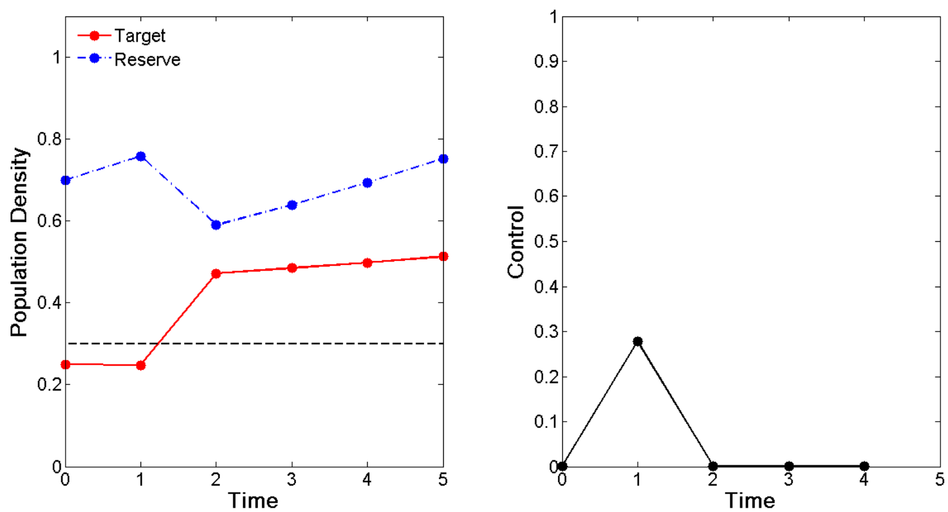
and thus the only augmentation occurs at the final time step $k = 4$ when 90% of the reserve population is translocated to the target population. Recall that 0.9 is the maximum possible value for any u_k. In this scenario we see that though the target population is augmented to be above its minimum threshold growth, $a = 0.3$ (see dashed black line in Figure 5.1(a)), at the final time, the proportion of the reserve population moved is so large that the reserve population falls below its minimum threshold for growth, $b = 0.3$. Indeed, the proportion translocated is so large, that the target population exceeds its carrying capacity at the final time, i.e. $x_T > 1$.

When these results are compared to results from the same parameters set using the discrete model in Chapter 4 (where the population is augmented before it grows in each time step), we see that the optimal augmentation strategy is qualitatively the same. However, note that in this model (grow then augment) the optimal proportion of the reserve population to translocate is the maximum allowable amount, while in the other discrete model (augment then grow) the optimal proportion of the reserve population to translocate is not the maximum amount (only 80%).

In the second scenario, we let $A_2 = 0.7$ and $B = 0.75$ (see Figure 5.1(b)). Thus, it is 75% as important to maximize the reserve population at the final time as it is to maximize the target population at the final time. The values for the optimal control in this scenario



(a) No importance in maximizing the reserve population, $B = 0$.



(b) Increased importance in maximizing the reserve population, $B = 0.75$.

Figure 5.1: Simulation for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.30$, $s = 0.70$, $p = 1$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 0.10$, and $A_2 = 0.70$. In (a) $B = 0$ and in (b) $B = 0.75$. The graphs on the left show the density of the target (red) and reserve (blue dashed) populations at each time step. The graphs on the right show the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control are (a) $u = [0.00\ 0.00\ 0.00\ 0.00\ 0.90]$, and (b) $u = [0.00\ 0.28\ 0.00\ 0.00\ 0.00]$.

are

$$u = [0.00\ 0.28\ 0.00\ 0.00\ 0.00],$$

and thus the only augmentation occurs at the final time step $k = 1$ when 28% of the reserve population is translocated to the target population. Comparing this to the previous scenario in Figure 5.1(a), we see that the reserve population is now harvested in such a way that it remains above its minimum threshold for growth, $b = 0.3$ (see dashed black line in Figure 5.1(b)), and that the target population is augmented in such a way that it falls between its minimum threshold for growth and its carrying capacity at the final time, i.e. $a = 0.3 < x_T < 1$. The difference between the two scenarios is that in the first scenario no importance was given to maximizing the reserve population at the final time, but in this scenario that importance was considerably increased (though still not as important as maximizing the target population at the final time).

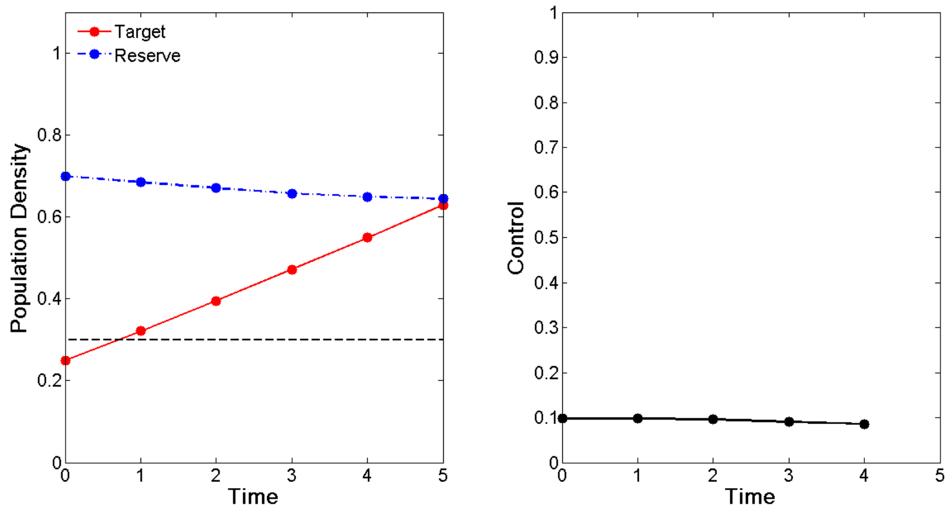
When these results are compared to results from the same parameters set using the discrete model in Chapter 4 (where the population is augmented before it grows in each time step), we see that the optimal augmentation strategy is qualitatively the same. However, note that in this model (grow then augment) the optimal time to translocate individuals from the reserve population to the target population occurs at time step $k = 1$, while in the other discrete model (augment then grow) the optimal time to translocate individuals occurs at time step $k = 2$. For both models, the resulting outcomes for both the target and reserve populations are similar.

In the second scenario, we let $A_2 = 0.5$ and $B = 0.25$ (see Figure 5.2(a)). Thus, it is 25% as important to maximize the reserve population at the final time as it is to maximize the target population at the final time. Additionally, note the cost coefficient A_2 is lower than in the previous two scenarios. The values for the optimal control in this scenario are

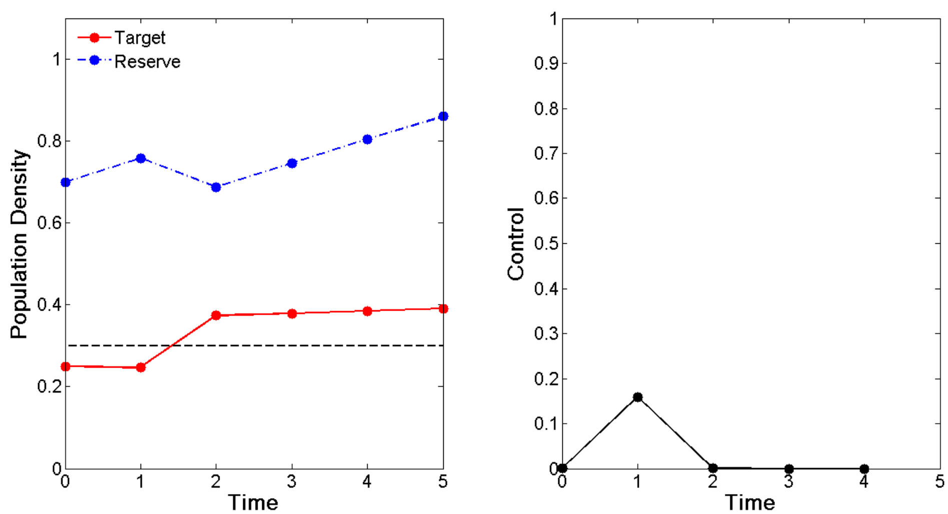
$$u = [0.10\ 0.10\ 0.10\ 0.09\ 0.09],$$

and thus a low level of augmentation occurs at each time step. For time steps $k = 0, 1, 2$, 10% of the reserve population is translocated to the target population, and at time step $k = 3, 4$, 9% of the reserve population is translocated. This maintained low level of augmentation is enough to augment the target population such that it rises above its minimum threshold for growth, $a = 0.3$ (see dashed black line in Figure 5.2(a)) by $k = 1$, and above 60% of its carrying capacity by the final time $T = 5$.

When these results are compared to results from the same parameter set using the discrete model in Chapter 4 (where the population is augmented before it grows in each time step), we see that the optimal augmentation strategy is qualitatively quite different. Using the other model (augment then grow), the optimal augmentation strategy was to translocate 50% of the individuals from the reserve population at time step $k = 3$ (a single augmentation). However, for this model (grow then augment) the optimal augmentation strategy is a low level of augmentation at every time step. This is an example of how a different order of events in a discrete model can lead to drastically different qualitative



(a) Lower cost of translocation, $A_2 = 0.50$.



(b) Higher cost of translocation, $A_2 = 0.80$.

Figure 5.2: Simulation for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.30$, $s = 0.70$, $p = 1$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 0.10$, and $B = 0.25$. In (a) $A_2 = 0.50$ and in (b) $A_2 = 0.80$. The graphs on the left show the density of the target (red) and reserve (blue dashed) populations at each time step. The graphs on the right show the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control are (a) $u = [0.10\ 0.10\ 0.10\ 0.09\ 0.09]$, and (b) $u = [0.00\ 0.16\ 0.00\ 0.00\ 0.00]$.

optimal controls. Note, however that in both discrete models, both the target and reserve populations are between the minimum threshold for growth and their carrying capacity at the final time, i.e. $a = 0.3 < x_T < 1$ and $b = 0.3 < y_T < 1$.

In the last of these scenarios, we let $A_2 = 0.8$ and $B = 0.25$ (see Figure 5.2(b)). Thus, it is 25% as important to maximize the reserve population at the final time as it is to maximize the target population at the final time. Additionally, note that the cost coefficient A_2 is higher than in the scenarios shown in Figure 5.1. The values for the optimal control in this scenario are

$$u = [0.00\ 0.16\ 0.00\ 0.00\ 0.00],$$

and thus the only augmentation occurs at time step $k = 1$ when 16% of the reserve population is translocated to the target population. This one time low level augmentation is high enough to raise the target population above its minimum threshold for growth by time step $k = 2$, and low enough to allow the reserve population to be larger at the final time, $T = 5$, than at the initial time, $t = 0$.

When these results are compared to results from the same parameter set using the discrete model in Chapter 4, we see that the optimal augmentation strategy is qualitatively the same. However, note that in this model (grow then augment) the optimal time to translocate individuals from the reserve population to the target population occurs at time step $k = 1$, while in the other discrete model (augment then grow) the optimal time to translocate individuals occurs at time step $k = 2$. For both models, the resulting outcomes for both the target and reserve populations are similar.

One should note, that if we let $A_2 = 0.9$ instead of $A_2 = 0.8$, then the optimal augmentation strategy becomes to do no augmentation at any time step. In this case, the cost of augmentation has become too high to implement. This is the exact same optimal strategy we see for the same parameter set using the discrete model in Chapter 4.

5.3.2 Varying the Intrinsic Growth Rate of the Reserve Population

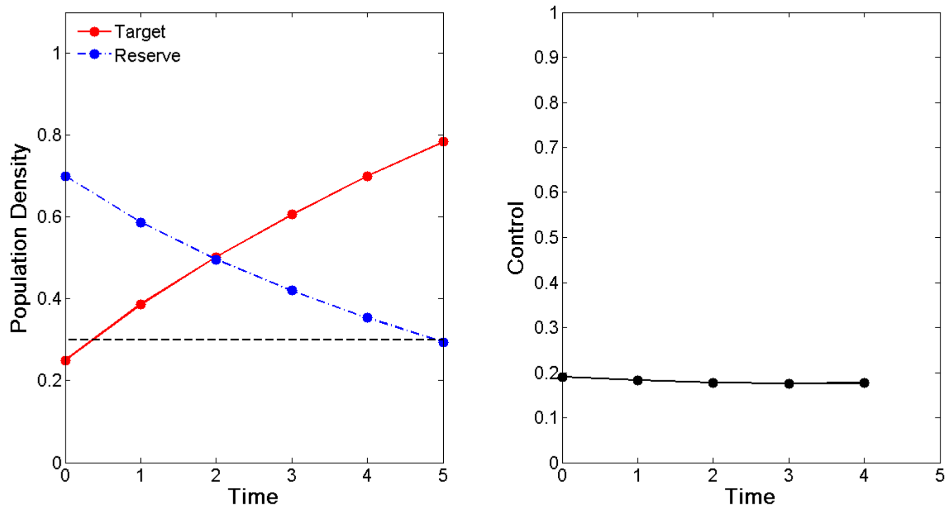
In the next set of scenarios, we consider the impact of varying the intrinsic growth rate of the reserve population, s. In these four scenarios we take $a = 0.3$, $b = 0.3$, $r = 0.25$, $p = 1$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 1$, $A_2 = 0$.

In these first two scenario we take $B = 0$ with $s = 0.3$ in Figure 5.3(a) and $s = 1.20$ in Figure 5.3(b). The optimal control for the scenario in Figure 5.3(a) is

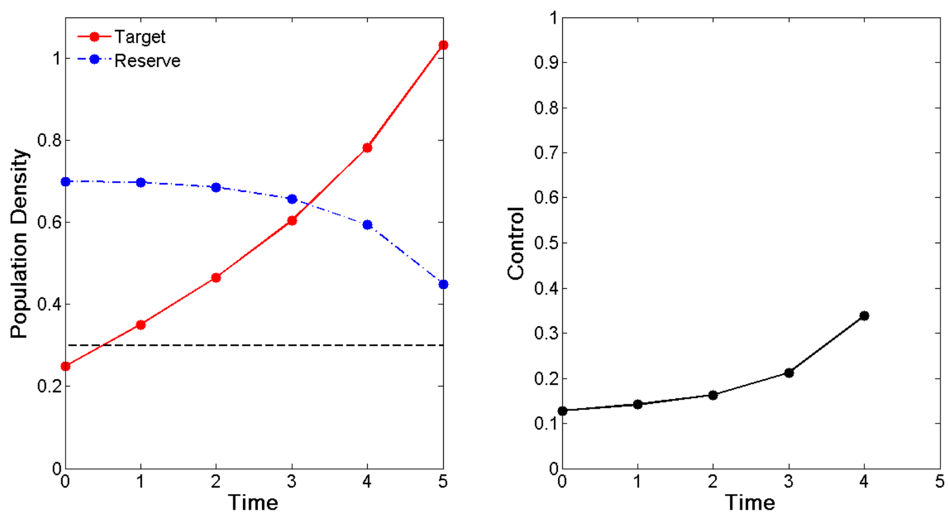
$$u = [0.19\ 0.18\ 0.18\ 0.18\ 0.18],$$

and thus a low level of augmentation occurs at each time step. Specifically, at time step $k = 1$, 19% of the reserve population is translocated to the target population, and at each remaining time step 18% is translocated. The optimal control for the scenario in Figure 5.3(b) is

$$u = [0.13\ 0.14\ 0.16\ 0.21\ 0.34],$$



(a) Lower intrinsic growth rate, $s = 0.30$.



(b) Higher intrinsic growth rate, $s = 1.20$.

Figure 5.3: Simulation for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.25$, $p = 1$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 1$, $A_2 = 0$, and $B = 0$. In (a) $s = 0.30$ and in (b) $s = 1.20$. The graphs on the left show the density of the target (red) and reserve (blue dashed) populations at each time step. The graphs on the right show the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control are (a) $u = [0.19\ 0.18\ 0.18\ 0.18\ 0.18]$, and (b) $u = [0.13\ 0.14\ 0.16\ 0.21\ 0.34]$.

and thus the augmentation starts at a low level and slowly rises over each of the time steps.

In the first scenario (with $s = 0.3$), the reserve population is harvested in such a way that at the final time the reserve population is exactly 30% of its carrying capacity. Recall, this is the minimum threshold for growth for the reserve population, $b = 0.3$. Since $y = b$ is an equilibrium for this discrete model, after the final time, the reserve population will remain at 30% of its carrying capacity. When we compare these results to results from the same parameter set using the discrete model in Chapter 4, we see that though the optimal augmentation strategies are roughly qualitatively similar, in the other discrete model (augment then grow) the reserve population is harvested in such a way that it falls below the minimum threshold for growth (see Figure 4.9(a)). In that case, after the final time, the reserve population will continue to decline to extinction.

In the second scenario (with $s = 1.2$), the target population is augmented such that it rises above its carrying capacity by the final time, i.e. $x_T > 1$. If we compare these results to the results from the same parameter set using the other discrete model (augment then grow, see Chapter 4), we see that the optimal augmentation strategies are qualitatively similar. However, using the other discrete model, the target population does not rise above its carrying capacity by the final time.

When we compare the results of both of these scenarios ($s = 0.3$ and $s = 1.2$) to results from a similar parameter set using the continuous model in Chapter 2 (see Figure 2.4), we see that the optimal control strategies and corresponding states are roughly qualitatively similar.

In these next two scenario we take $B = 0.75$ with $s = 0.3$ in Figure 5.4(a) and $s = 1.20$ in Figure 5.4(b). The optimal control for the scenario in Figure 5.4(a) is

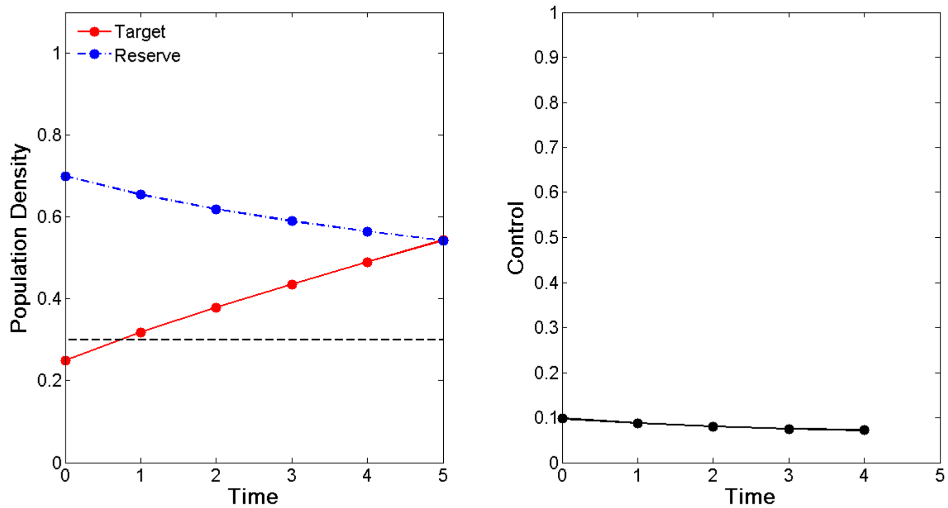
$$u = [0.10\ 0.09\ 0.08\ 0.08\ 0.07],$$

and thus a low level of augmentation occurs at each time step, slightly decreasing the level of augmentation over time. The optimal control for the scenario in Figure 5.4(b) is

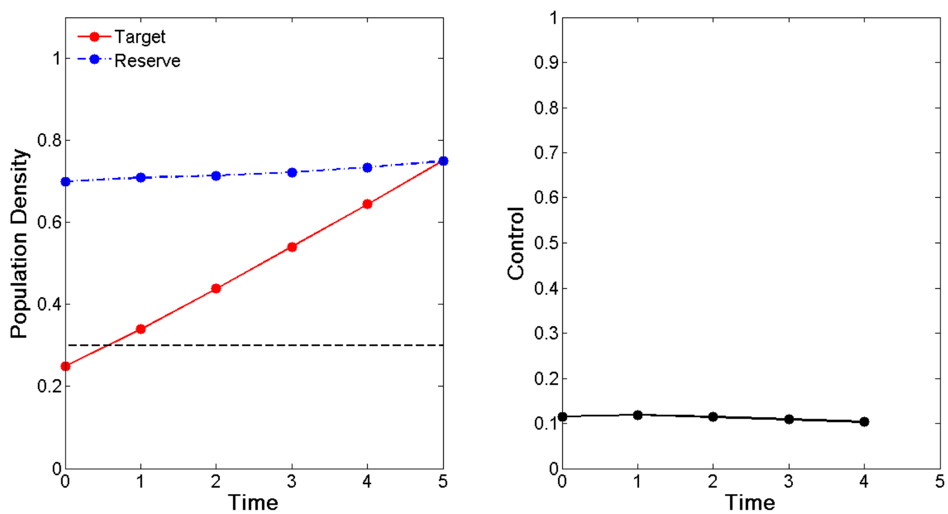
$$u = [0.12\ 0.12\ 0.11\ 0.11\ 0.10],$$

and thus we see the same qualitative augmentation strategy for when $s = 0.3$ to maintain a low level of augmentation at each time step, slightly decreasing the level of augmentation over time.

In both scenarios, we see that the reserve population is harvested in such a way that the population is between its minimum threshold for growth, $b = 0.3$ (see dashed black lines in Figures 5.4(a) and 5.4(b)), and its carrying capacity at the final time, i.e. $b = 0.3 < y_T < 1$. Additionally, in both scenarios, the target population is augmented in such a way that the population is between its minimum threshold for growth, $a = 0.3$ and its carrying capacity at the final time, i.e. $a = 0.3 < x_T < 1$. Compared to the previous two scenarios in Figure 5.3 when $B = 0$, we see that increasing the importance of maximizing the reserve population at the final time to $B = 0.75$ prevents over-harvesting the reserve population when the reserve



(a) Lower intrinsic growth rate, $s = 0.30$.



(b) Higher intrinsic growth rate, $s = 1.20$.

Figure 5.4: Simulation for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.25$, $p = 1$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 1$, $A_2 = 0$, and $B = 0.75$. In (a) $s = 0.30$ and in (b) $s = 1.20$. The graphs on the left show the density of the target (red) and reserve (blue dashed) populations at each time step. The graphs on the right show the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control are (a) $u = [0.10\ 0.09\ 0.08\ 0.08\ 0.07]$, and (b) $u = [0.12\ 0.12\ 0.11\ 0.11\ 0.10]$.

intrinsic growth rate is low ($s = 0.3$, see Figure 5.3(a)), and over-augmenting the target population when the reserve intrinsic growth rate is high ($s = 1.2$, see Figure 5.3(b)).

When we compare these results to the results from the same parameter set using the other discrete model (augment then grow, see Chapter 4), we see that the qualitative optimal augmentations strategies for each discrete model are slightly different for $s = 1.2$. Specifically, when $s = 1.2$, we see an increase in the proportion of the reserve population translocated over the entire time horizon in the other discrete model (augment then grow), while we see a decrease over the entire time horizon in proportion of the reserve population translocated when using this discrete model (grow then augment). The difference between the optimal augmentation strategy in each model combined with the difference between the order of events in each discrete model, leads to slightly different behaviors in the target and reserve populations. This is most easily seen when $s = 1.2$. In this discrete model (grow then augment) the reserve and target populations have roughly the same population density (about 75% of their carrying capacities) at the final time. However, in the other discrete model (augment then grow), there is a large difference in the population densities of the target and reserve population at the final time, $x_T = 0.65$ and $y_T = 0.85$.

When we compare the results of both of these scenarios ($s = 0.3$ and $s = 1.2$) to results from a similar parameter set using the continuous model in Chapter 2 (see Figure 2.5), we see that the optimal control strategies and corresponding states are roughly qualitatively similar.

5.3.3 Varying the Time Horizon

In the next two scenarios, we consider the impact of changing the time horizon during which augmentation can occur (i.e. changing T). In these two scenarios we take $a = 0.3$, $b = 0.3$, $r = 0.25$, $s = 1.20$, $p = 1$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 20$, $A_2 = 0$, and $B = 0.75$.

In the first of these two scenarios we let $T = 5$ (see Figure 5.5(a)), while in the second scenario we let $T = 10$ (see Figure 5.5(b)). The optimal control for the scenario in Figure 5.5(a) is

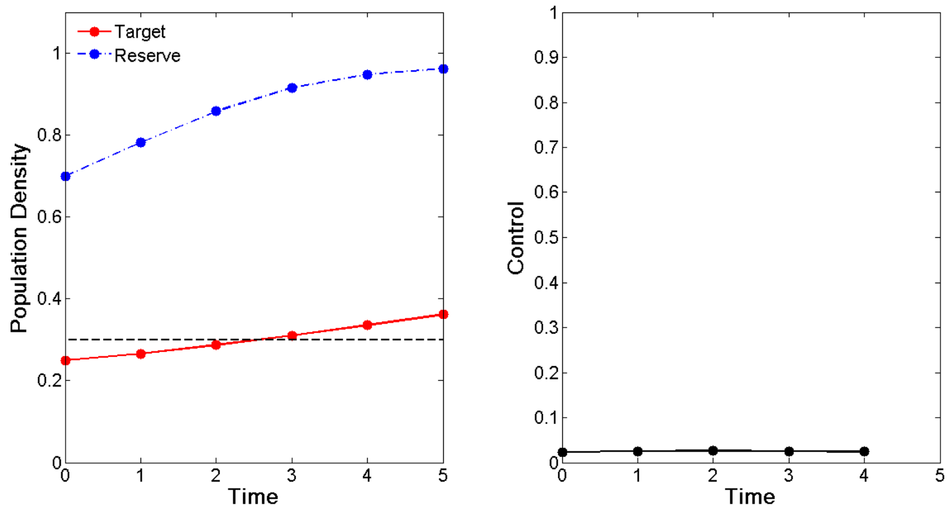
$$u = [0.02\ 0.03\ 0.03\ 0.03\ 0.02],$$

and thus we see a small proportion of the reserve population is translocated to the target population at each time step (either 2% or 3% of the reserve population). The optimal control for the scenario in Figure 5.5(b) is

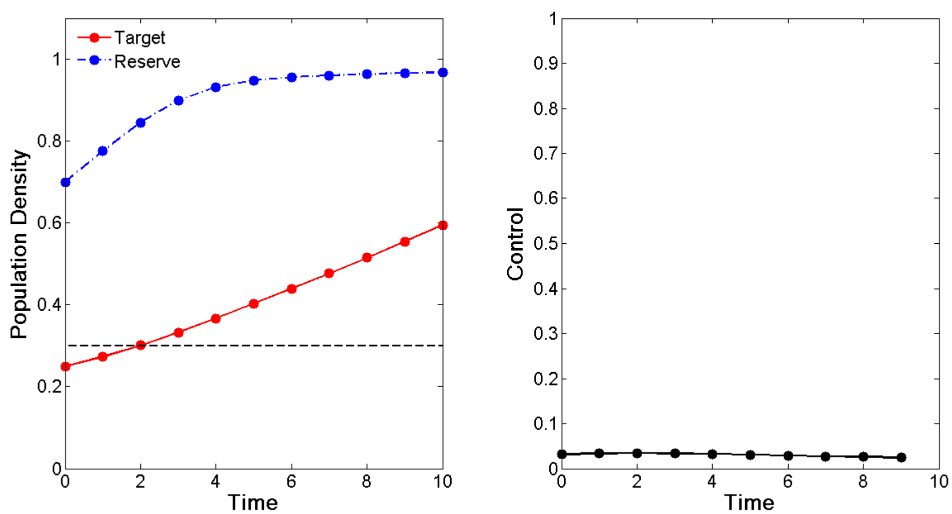
$$u = [0.03\ 0.03\ 0.03\ 0.03\ 0.03\ 0.03\ 0.03\ 0.03\ 0.03\ 0.02],$$

and thus we see the same qualitative augmentation strategy as when $T = 5$ (Figure 5.5(a)), however, the low level of augmentation is maintained over the entire time horizon of 10 time steps, $k = 0, \ldots, 9$.

When we compare the results of both of these scenarios ($T = 5$ and $T = 10$) to results from a similar parameter set using the continuous model in Chapter 2 (see Figure 2.2), we



(a) Shorter time horizon, $T = 5$.



(b) Higher time horizon, $T = 10$.

Figure 5.5: Simulation for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.25$, $s = 1.2$ $p = 1$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 20$, $A_2 = 0$, and $B = 0.75$. In (a) $T = 5$ and in (b) $T = 10$. The graphs on the left show the density of the target (red) and reserve (blue dashed) populations at each time step. The graphs on the right show the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control are (a) $u = [0.02\ 0.03\ 0.03\ 0.03\ 0.02]$, and (b) $u = [0.03\ 0.03\ 0.03\ 0.03\ 0.03\ 0.03\ 0.03\ 0.03\ 0.03\ 0.02]$.

see that the optimal control strategies and corresponding states are roughly qualitatively similar.

5.3.4 Varying the Ratio of the Reserve Carrying Capacity to the Target Carrying Capacity

In the next four scenarios, we consider the effect of varying the ratio of the reserve population carrying capacity to the target population carrying capacity. When $p < 1$, the reserve carrying capacity is smaller than the target carrying capacity. Thus, $p = 0.5$ could represent when the reserve population is generated from a captive breeding program or zoo population. When $p > 1$, the reserve carrying capacity is larger than the target carrying capacity. Thus, $p = 1.2$ could represent when the reserve population is a wild, stable (and possibly protected) population. For these four scenarios, we let $a = 0.3$, $b = 0.3$, $r = 0.25$, $s = 1.20$, $x_0 = 0.25$, $y = 0.75$, $A_2 = 0$, and $B = 0$.

In these first two scenarios we take $A_1 = 1$ with $p = 0.50$ in Figure 5.6(a) and $p = 1.20$ in Figure 5.6(b). The optimal control for the scenario in Figure 5.6(a) is

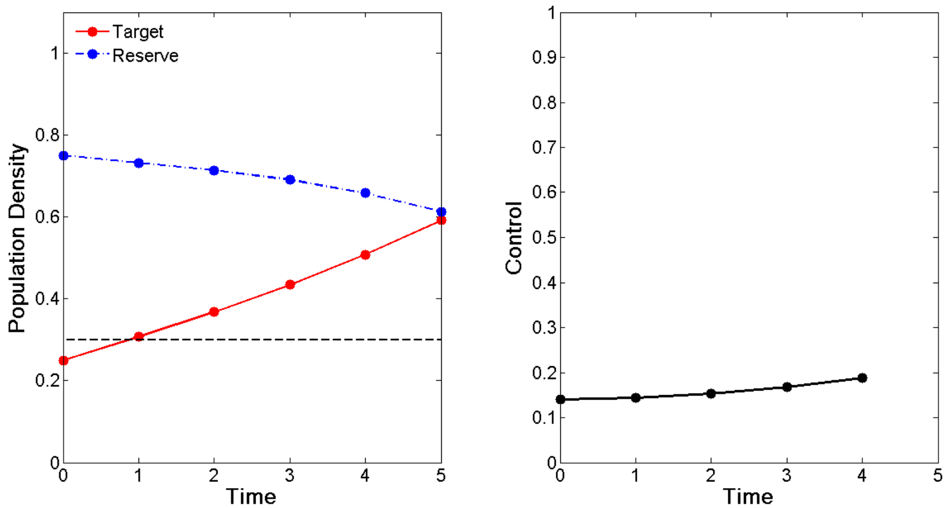
$$u = [0.14\ 0.14\ 0.15\ 0.17\ 0.19],$$

that is, a small proportion of the reserve population (less than 20%) is translocated to the target population at each time step with a slight increase in the proportions over the time horizon. The optimal control for the scenario in Figure 5.6(b) is

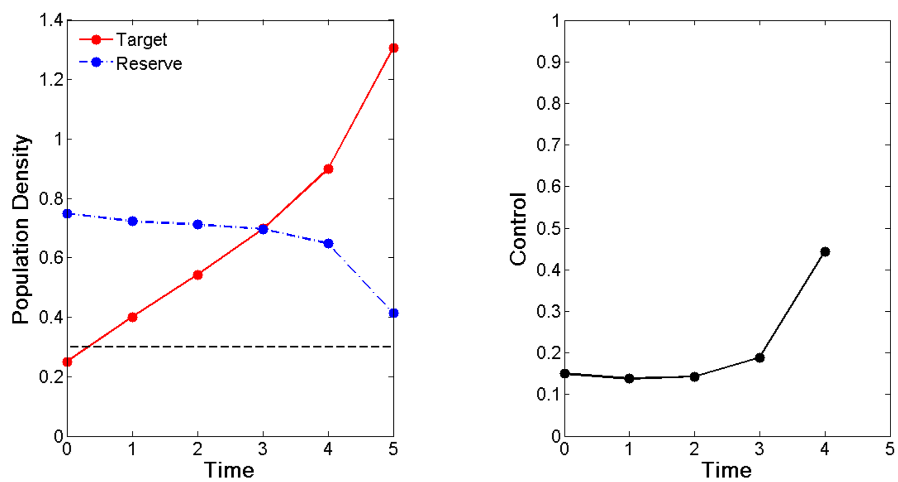
$$u = [0.15\ 0.14\ 0.14\ 0.19\ 0.44],$$

that is, for time steps $k = 0, 1, 2, 3$, a small proportion of the reserve population (less than 20%) is translocated to the target population, however at time step $k = 4$ a significantly larger proportion, 44%, of the reserve population is translocated. Notice, that for the lower ratio $p = 0.5$, the low level of augmentation at each time step is sufficent to raise the target population to almost 60% of its carrying capacity by the final time (well above its minimum threshold for growth), while only reducing the reserve population to roughly 60% of its carrying capacity at the final time. Thus, both the target and reserve population are between their minimum thresholds for growth and their carrying capacities at the final time. For the larger ratio $p = 1.20$, the increased augmentation at time step $k = 4$, translocating 44% of the reserve population to the target population, raises the target population well above its carrying capacity to roughly 130% of its carrying capacity.

When we compare the results for $p = 0.5$ to results from the same parameter set using the other discrete model (augment then grow) in Chapter 4 (see Figure 4.11), we find that both models produce a similar qualitative optimal augmentation strategy of translocating between 10% and 20% of the reserve population at each time step to the target population with a slight increase in the proportions over the time horizon. When we compare the results for $p = 0.5$ to results from a similar parameter set using the continuous model in Chapter 2 (see Figure 2.6), we see that the optimal control strategies and corresponding



(a) Lower ratio of reserve carrying capacity to target carrying capacity, $p = 0.50$.



(b) Higher ratio of reserve carrying capacity to target carrying capacity, $p = 1.20$.

Figure 5.6: Simulation for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.25$, $s = 1.20$, $x_0 = 0.25$, $y_0 = 0.75$, $A_1 = 1$, $A_2 = 0$, and $B = 0$. In (a) $p = 0.50$ and in (b) $p = 1.20$. The graphs on the left show the density of the target (red) and reserve (blue dashed) populations at each time step. The graphs on the right show the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control are (a) $u = [0.14\ 0.14\ 0.15\ 0.17\ 0.19]$, and (b) $u = [0.15\ 0.14\ 0.14\ 0.19\ 0.44]$.

states are roughly qualitatively similar. In the continous case, the values for the control over are not strictly increasing with time.

When we compare the results for $p = 1.20$ to results from the same parameter set using the other discrete model (augment then grow) in Chapter 4 (see Figure 4.12), we see that the qualitative optimal augmentation strategies produced by each model are not similar. For this model (grow then augment), the values for the control were not strictly increasing with time, and there was a dramatic increase in the proportion of the reserve population translocated at time step $k = 4$. However, in the other discrete model (augment then grow), the values for the control are strictly increasing with time, and there is no dramatic increase in the proportion translocated at time step $k = 4$. The optimal augmentation strategy in the other discrete model (augment then grow) does cause the target population to exceed its carrying capacity by the final time, however, by a considerably smaller amount, $x_T = 1.07$. Thus, in the other discrete model the target population only reaches 107% of its carrying capacity, as opposed to the 130% it reaches in this model (grow then augment).

The previous two scenarios are similar to the previous two scenario except that we have increased the cost of translocation by a factor of 20, i.e. we let $A_1 = 20$ (recall $A_1 = 1$ in the previous two scenarios). The results for these last two scenarios are shown in Figure 5.7 where $p = 0.50$ in 5.7(a) and $p = 1.20$ in 5.7(b). For the scenario shown in Figure 5.7(a), the optimal control is

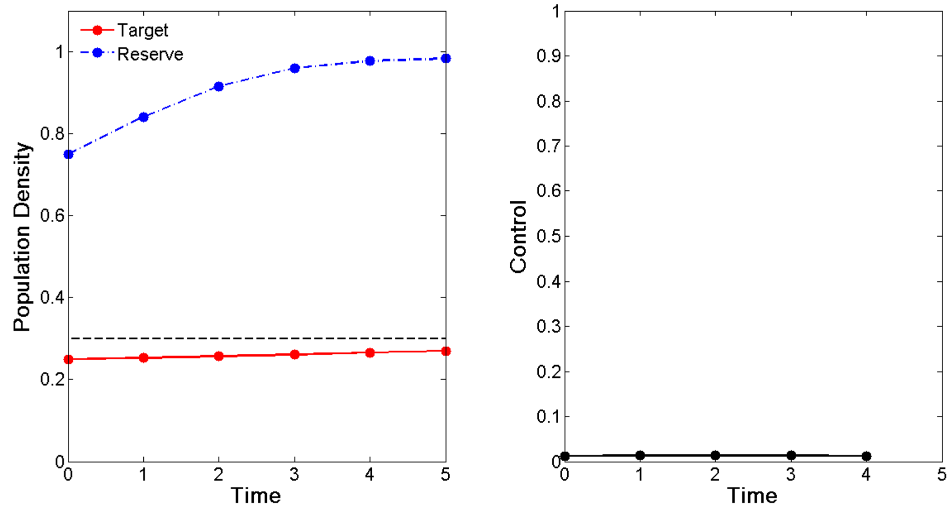
$$u = [0.01\ 0.01\ 0.01\ 0.01\ 0.01],$$

that only 1% of the reserve population is translocated to the target population at each time step. For the scenario shown in Figure 5.7(b), the optimal control is

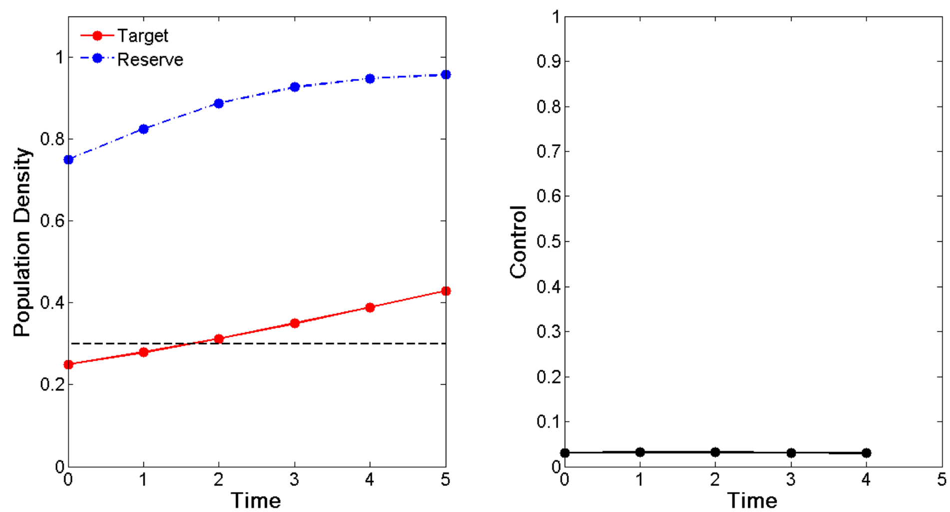
$$u = [0.03\ 0.03\ 0.03\ 0.03\ 0.03],$$

that is 3% of the reserve population is translocated to the target population at each time step.

If we compare the results of these two scenarios to the results of the previous two scenarios, we see the impact of increasing the cost of translocation by a factor of 20 for different ratios of the reserve carrying capacity to the target carrying capacity. In the case where $p = 0.50$, increasing the cost of translocation by a factor of 20 prevented enough augmentation to enable the target population to rise above its minimum threshold for growth, $a = 0.3$ (see black dashed line in Figure 5.7(a) by the final time. The higher cost of translocation resulted in lower proportions of the reserve population being translocated (14-19% when $A_1 = 1$, but only 1% when $A_1 = 20$). In the case where $p = 1.2$, increasing the cost of translocation by a factor of 20 does not prevent the target population from rising above its minimum threshold for growth, $a = 0.3$ (see black dashed line in Figure 5.7(b)). However, does results in the target population at the final time being much lower. When $A_1 = 1$, the target population was augmented such that it rises above its carrying capacity by the final time, but when $A_1 = 20$, the target population only rises to 43% of its carrying



(a) Lower ratio of reserve carrying capacity to target carrying capacity, $p = 0.50$.



(b) Higher ratio of reserve carrying capacity to target carrying capacity, $p = 1.20$.

Figure 5.7: Simulation for the discrete optimal control of augmentation where the population is augmented before growth in which the parameters are $a = 0.30$, $b = 0.30$, $r = 0.25$, $s = 1.20$, $x_0 = 0.25$, $y_0 = 0.75$, $A_1 = 20$, $A_2 = 0$, and $B = 0$. In (a) $p = 0.50$ and in (b) $p = 1.20$. The graphs on the left show the density of the target (red) and reserve (blue dashed) populations at each time step. The graphs on the right show the proportion of the reserve population used to augment the target population at each time step. Note the values for the optimal control are (a) $u = [0.01\ 0.01\ 0.01\ 0.01\ 0.01]$, and (b) $u = [0.03\ 0.03\ 0.03\ 0.03\ 0.03]$.

capacity. Again, we see the higher cost of translocation resulting in lower proportions of the reserve population being translocated (14-44% when $A_1 = 1$, but only 3% when $A_1 = 20$).

5.4 Conclusions

In this chapter we analyzed an optimal control formulation for species augmentation which utilizes a discrete time difference equation model to describe the dynamics of the target and reserve populations. For the discrete model in this chapter we assume the order of events at each time step is that the population grows (via natural reproduction) before it is augmented. Note that using this formulation of the discrete time model, we were able to utilize Pontryagin's Maximum Principle to determine the necessary conditions for an optimal control and to derive a characterization for an optimal control. In Section 5.3 we explored the numerical results for several different illustrative parameter sets. Several sets of these results were compared to results from scenarios with similar parameter sets from Chapter 2 and/or Chapter 4.

In Section 5.3.1 we investigated the impact of varying the cost of translocation by varying the values of the cost coefficients A_1 and A_2. As in Chapter 4 we found that the importance of maximizing the reserve population may need to be increased (at least nonzero) in order to maintain the reserve population above its minimum threshold for growth (compare Figures 5.1(a) and 5.1(b)). In fact, the optimal augmentation strategies for the scenarios in Figures 5.1(a) and 5.1(b) are qualitatively the same as the optimal augmentation strategies for the scenarios with the same parameters in Chapter 4 (see Figures 4.1 and 4.2). However, when the cost coefficient A_2 was lowered to 0.5 in Figure 5.2(a) (as opposed to $A_2 = 0.7$ in Figures 5.1(a) and 5.1(b)), we found an optimal augmentation strategy that was quite qualitatively different from both those found in Figures 5.1(a) and 5.1(b). More intriguingly, the optimal augmentation strategy was qualitatively different from the scenario with the same parameters in Chapter 4 (see Figure 4.3). This scenario (Figure 5.2(a)) is an example of how a different order of events in a discrete model can lead to drastically different optimal controls. Thus, in seeking an optimal augmentation strategy, it is important that natural resource managers determine whether they will be augmenting before or after the breeding seasons. It should be noted that the lower cost of augmentation ($A_2 = 0.5$ as opposed to $A_2 = 0.7$) did lead to an optimal control strategy that translocated a larger proportion of the reserve population than did the higher cost of augmentation. Though the proportion translocated at each time step is lower, since an translocation occurs at each time step, the effective total proportion of the reserve population moved is greater. Lastly, in Section 5.3.1 we saw, as in Chapter 4, that increasing the linear cost coefficient to $A_2 = 0.8$ leads to a qualitatively similar optimal augmentation strategy as when $A_2 = 0.7$, however the proportion translocated at the single time step is lower.

Next, in Section 5.3.2, we considered the effect of varying the intrinsic growth rate of the reserve population, s. Here, as in Chapters 2, 3, and 4, we observed that if the intrinsic growth rate of the reserve population is low enough, the reserve population will not be able to reproduce enough individuals to replace those being harvested for translocation. In Chapters 3 and 4 we saw examples where a low intrinsic growth rate for the reserve population led to the reserve population being harvested such that it falls below its minimum threshold for growth by the final time and will thus inevitably decline to extinction (see Figures 3.1(a), 3.1(b), and 4.9(a)). However, in this chapter for the parameter set with the low intrinsic growth rate the reserve population is harvested such that it is exactly at its minimum threshold for growth at the final time (see Figure 5.3(a)). Thus, after the final time the reserve population will remain at this equilibrium and not decline to extinction. One should note that using the same parameters and the other discrete model (augment then grow, see Figure 4.9(a)) leads to the inevitable extinction of the reserve population, despite the fact the optimal augmentation strategy for both scenarios are similar. Despite the slight difference between the optimal augmentation strategies, the difference between the order of events between the two discrete models leads to very different outcomes for the reserve population. Thus, again we see that it is important for those planning augmentations to take into account whether augmentations will occur before or after the breeding seasons, as this can make a differential impact on the lastly outcome to the reserve and target populations.

In Section 5.3.2, as in Chapters 2, 3, and 4, we also observed that increasing the importance of maximizing the reserve population at the final time, i.e. increasing the value of B, can prevent over-harvesting the reserve population so that both the reserve and target populations inevitably reach carrying capacity. Thus, we see the recurring theme from each of the different optimal control formulations, that natural resource managers must consider the importance of maximizing the reserve population at the final time if they wish to keep from over-harvesting the reserve population. Again, by over-harvesting, we mean harvesting the reserve population such that it falls at or below its minimum threshold for growth by the final time. It should be noted that the optimal augmentation strategies for all of the scenarios in Section 5.3.2 were at least roughly qualitative similar to those generated from similar (or the same) parameter sets using both the continuous model in Chapter 2 and the other discrete model (augment then grow) in Chapter 4.

Next, in Section 5.3.3, we examined how varying the time horizon, T, affects the optimal augmentation strategy. The two scenarios we considered in this section (see Figure 5.5) had parameters similar to two continuous time scenarios from Chapter 2 (see Figure 2.2). In the two scenarios shown in Figure 5.5, doubling the time time horizon (from $T = 5$ to $T = 10$) did not seem to affect the qualitative optimal augmentation strategy which was to translocate a small proportion (2% or 3%) of the reserve population at each time step. However, for the scenario with the extended time horizon, $T = 10$, the target population was at a much higher density than when $T = 5$. It should be noted though, that in both cases, $T = 5$ and $T = 10$, the target population at the final time is between its minimum threshold for growth and its carrying capacity and thus will increase to its carrying capacity after the final time. Therefore, the long term outcome for the target population in both scenarios is the same. In order to better understand the effects of varying the time horizon, one could consider varying some of the other parameters in addition to varying the time horizon, and see how the optimal augmentation strategy is affected in each case.

Lastly, in Section 5.3.4, we considered the impact of varying the ratio of the reserve carrying capacity to the target carrying capacity, p. We considered scenarios where $p < 1$ (the reserve carrying capacity is *smaller* than the target carrying capacity), as well as scenarios where $p > 1$ (the reserve population carrying capacity is *larger* than the target carrying capacity). From these scenarios, we observed, as in Chapters 3 and 4, that when $p < 1$ lower proportions of the reserve population are translocated to the target population than when $p > 1$. When we compared results of scenarios to those using the same parameter sets (with $p > 1$) from Chapter 4 (compare Figure 5.6(b) to Figure 4.12) we saw another example of the difference in the discrete models' order of events leading to qualitative dissimilar augmentation strategies. It should be noted that when comparing results to those form Chapter 4 with $p < 1$ and all other parameters equal (compare Figure 5.6(a) to Figure 4.11), the optimal augmentation strategies were qualitatively similar. From the last two scenarios in Section 5.3.4, we discovered that an increase in the cost of augmentation (via an increase to the cost coefficient A_1), can lead to not being able to augment the target population such that it rises above its minimum threshold for growth by the final time in the case where $p < 1$ (compare Figure 5.7(a) with high cost to Figure 5.6(a) with low cost). This is due to the fact that when $p < 1$, and the reserve population carrying capacity is smaller than the target population carrying capacity, a larger proportion of the reserve population has to be translocated to have the same effect on the target population density as when $p \geq 1$. Thus, when the cost of augmentation becomes more costly and lower proportions of the reserve population are being translocated, it may not be enough to boost the target population above its minimum threshold for growth.

It is important to note that of the scenarios in this chapter that we could compare to scenarios in Chapter 2, the optimal augmentation strategies were qualitatively similar. However, of the scenarios in this chapter that we could compare to the other discrete model (augment then grow) in Chapter 4, the optimal augmentation strategies were sometimes qualitatively similar and sometimes qualitatively different. These differences in qualitative augmentation strategies among the same parameter sets for discrete models with different order of events, highlight the fact that it is important to choose the discrete model with the order of events that is most representative of what occurs in the natural system being modeled. In the case of species augmentation, the discrete model where augmentation occurs before the population grows in each time step corresponds to natural resource managers augmenting a population before a growing season. This is likely most appropriate when reproductively mature individuals are being augmented into the target population. However, the discrete model where the population growth occurs before the augmentation in each time step corresponds to augmenting a population after the breeding season. This is likely more appropriate when juveniles from a captive breeding program are being augmented into the target population in hopes of their being raised in the wild.

Chapter 6

Future Extensions

The work in this dissertation presents the first optimal control problems which examine the conservation method of species augmentation and attempt to develop optimal augmentation strategies given various constraints. We investigate optimal control problems which utilize ordinary differential equations and discrete difference equations to model the underlying population dynamics. In comparing the optimal control formulations used in each chapter, we found that the type of model used and the format of the objective functional have a large impact on the optimal augmentation strategy. Thus, it is quite important to select the most appropriate model and objective functional when utilizing optimal control theory to develop augmentation strategies. Though these models are a crucial first step in modeling species augmentation in an control framework, there are many extensions which have yet to be explored.

6.1 Structured Populations

One avenue to investigate in future modeling of species augmentation using optimal control is to add structured populations to the model. The structure could be by age/stage, sex, and/or trait. Augmentation field experiments have shown it is often advantageous to augment the target population with only individuals of one sex, at a certain stage in their life cycle, or with a certain advantageous trait [27, 38]. Indeed, in the case of both the Florida panther augmentation and the Cabinet Mountain grizzly bear augmentation, only females of a reproductive age range were selected for the augmentations [27, 38]. By adding an optimal control component to existing structured models, optimal augmentation strategies could be developed for natural resource managers working with populations where the population structure is a key concern within the augmentation.

6.2 Other Populations

The population models considered in this dissertation contained only two populations, a target population (to augment) and a reserve population (to harvest individuals). However, it may be appropriate to model other populations that interact with both the target and reserve populations. For example, if the target population feeds primarily on a specific prey, it may be necessary to model the prey population as well since over augmenting the target population could lead to over-feeding on the prey, possibility leading to extinction. Other populations worth modeling would be

- population(s) with which the target population is in competition,
- population(s) with which the target population has a dependent mutualistic relationship, or
- invasive species population(s) which has out competed the target population and led to its decline.

Each of these scenarios requires the addition of one or more populations to the dynamical system modeling the underlying population dynamics. As more populations are added, different conservation strategies can be developed. For example, if an invasive species were being modeled, one could consider two controls, the first control being the proportion of the reserve population to augment into the target population at each time step, and the second being some amount of eradication effort in removing the invasive species.

6.3 Spatial Dynamics

Another possible extension for the models presented in this dissertation is to add spatial dynamics. In the augmentation projects that have been carried out, much consideration has been given to the best location to release translocated individuals into the target populations. This is especially crucial with territorial species. In modeling the spatial dynamics of the target population, one could develop spatially explicit augmentation strategies. That is, these models could be used to answer natural resource managers questions of "where is the *best location* to release translocated individuals in the target population range?" When considering adding spatial dynamics to a model, one must choose between modeling space continuously or discretely. If the population's temporal and spatial dynamics are both modeled continuously, then a partial differential equation (PDE) model is appropriate. Optimal control theory applied to PDEs has not been used extensively for natural resource management, and has the potential to provide many new insights for conservation policy. If the population's temporal and spatial dynamics are both modeled discretely, then a difference equation model is appropriate. Very few biological applications have been treated with optimal control for models which are discrete in time and space.

6.4 Stochasticity

Random catastrophic events are often highly detrimental to endangered populations, especially those with small population size or density. Additionally, randomly changing environmental features can also impact populations. Another interesting extension to the models presented in this dissertation would be to add stochasticity to the models to simulate either random catastrophic events or random environmental features. One extension might be to assume that the populations' intrinsic growth rate or carrying capacities are randomly changing over time. If using a PDE model in a heterogeneous environment, the diffusion and advection coefficients could have random features.

6.5 Other Objective Functionals

One extension to consider that does not change the underlying population models used is to consider other objective functionals. In the previous chapters we explored objective functionals which maximized the target population at the final time, maximized the reserve population at the final time (though weighted as less important than maximizing the target population), and minimized the costs associated with augmentation. It may be important to the natural resource managers to maximize the target and/or reserve population over the entire time horizon. In each of the objective functionals we took the cost associated with augmentation to be either a linear function, quadratic function, or linear plus quadratic function of the control. It is worth further investigation as to whether these are the most appropriate formats for the costs associated with augmentation.

6.6 Hybrid Control Models

For some populations, it may be most useful to model the population dynamics in continuous time, but only allow discrete augmentation events. In this case, a type of hybrid control model would be necessary. For these types of hybrid control models, the number of discrete augmentation events would be set (defined by the natural resource managers), but optimal control theory would be used to find the ideal time for these augmentation events to occur and what proportion of the reserve population would be moved in each augmentation event.

6.7 Modeling Population Size Directly

For the optimal control formulations considered here which used discrete time to model the underlying population dynamics, the issue of fractional individuals was ignored, largely because the discrete difference models used tracked population densities, not individuals. One could model the number of individuals directly, however, in this case it would be important to consider how to handle fractional individuals. That is, if the optimal augmentation strategy indicated that 20% of the reserve population needs to be translocated to the target population at a particular time step, the numerical method would need to have a scheme for translating this proportion into a whole number of individuals. This would change the numerical method being used, and is worth further investigation.

6.8 Further Investigation of Captive Breeding

Throughout the dissertation, we mention that one of the sources for a reserve population could be a captive breeding program. However, the introduction of captive bred individuals is not always successful. It is worth investigating the trade-off between removing individuals from the wild for captive breeding as opposed to leaving them in their natural habitat with the assumption that the efforts of captive breeding and reintroduction/augmentation may not be successful, and that the wild population may recover on its own. Models for captive breeding with optimal reintroduction/augmentation strategies could be compared to models where an endangered wild population is left in their natural habitat under various different scenarios. To add another layer of complexity, one could also consider models where an endangered wild population is left in their natural habitat, but conservation efforts are made to protect or improve that natural habitat. Examination and comparison of these types of models could help natural resource managers determine under what conditions a captive breeding program is most likely to be the most beneficial conservation strategy.

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Vita

Erin Nicole Bodine was born in Culver City, Califonia on June 21, 1981. After graduating from Sherman Oak Center for Enriched Studies in June 1999 she went to community colleges (Glendale Community College and Pasadena City College) for two years before transferring to Harvey Mudd College. She graduated in May 2003 from Harvey Mudd with a Bachelor of Science in Mathematics and a Bachelor of the Arts in Anthropology.

After obtain her bachelor degrees, Bodine worked for the Summer of 2003 at Philmont Scout Ranch in Cimmaron, New Mexico. It was there she met her future husband, Mac Bryan Barnes, a Tennessee native and student at the University of Tennessee, Knoxville (UT) majoring in Plant & Soil Science.

From August 2003 to July 2005 in the Biomathematics Department at the University of California, Los Angeles as a research assistant and lab manager for Dr. Sally Blower. While there Bodine worked on modeling the spread of infectious diseases. This work led to the publication of several journal articles, six of which Bodine is a co-author. The excitement and fulfillment of academic research led her to apply for graduate school in Mathematics. She learned of the Math Ecology program at UT from Barnes.

In August 2005, Bodine moved to Knoxville to begin attending UT in pursuit of a PhD in Mathematics with a concentration in Mathematical Ecology. Her first year of graduate school was supported by a graduate research assistantship through an NSF grant awarded to Dr. Suzanne Lenhart and Lou Gross of the Mathematics and Ecology Departments. This work done on this research assistantship led to the beginnings of modeling species augmentation. From August 2006 to August 2009, Bodine's graduate schooling was supported by a graduate teaching assistantship. On this teaching assistantship, she taught several semesters of a Math for Life Sciences course. Involvement with this course led to the development of a course textbook with Drs. Lenhart and Gross. Bodine was award a graduate research fellowship from the National Institute for Mathematical and Biological Synthesis which supported her graduate studies from August 2009 to July 2010. With the aid of this fellowhship Bodine finished her dissertation work and the majority of the development of the textbook.

Bodine graduated with her PhD in Mathematics with a concentration in Mathematical Ecology in August 2010. She continues her work in mathematical ecology and in teaching mathematics as an Assistant Professor at Rhodes College in Memphis, Tennessee.